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On the tribal classification of the Nearctic Melolonthinae (Coleoptera: Scarabaeidae), with descriptions of new species of *Acoma* Casey, 1889

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Abstract

The subfamily Melolonthinae (Coleoptera: Scarabaeidae) is defined and characterized, and a brief summary of the world melolonthine tribes and their distributions are provided. Nearctic genera previously considered *incertae sedis* (*Acoma* Casey, 1889, *Chaunocolus* Saylor, 1937 and *Chnaunanthus* Burmeister, 1844, *Phobetus* LeConte, 1856, and *Warwickia* Smith & Evans, 2005) are each placed in the proposed **new tribes** Acomini, Chnaunanthini, Phobetusini, and Warwickiini, respectively. Tribal assignments for all Nearctic melolonthine genera are presented. *Acoma chihuahuaensis*, *A. eusexfoliata*, *A. nonglabrata*, and *A. pararobusta* are all **new species** described from Mexico. The only known example of a female *Acoma*, represented by a specimen of *A. knulli* Howden, 1958, is figured and characterized. The generic composition of the Nearctic Melolonthini and Rhizotrogini is examined. *Madiniella* Chalumeau & Gruner, 1976, previously placed in Tanyproctini, is transferred to Rhizotrogini. The subfamilies Oncerinae and Podolasiinae are each removed as tribes from the Melolonthinae and elevated to the subfamily level within Scarabaeidae. The subtribe Triodonina is placed in synonymy with the tribe Rhizotrogini. An updated generic checklist and tribal key of the Nearctic Melolonthinae are provided.

Key words: *Chaunocolus*, *Chnaunanthus*, *Madiniella*, Mexico, *Oncerus*, Oncerinae, *Phobetus*, *Podolasia*, Podolasiinae, *Podostena*, Rhizotrogini, United States, *Warwickia*

Introduction

It has been 163 years since LeConte (1856) published the first study on the higher classification of the Nearctic Melolonthinae. Many of the earlier authors who worked on North American Melolonthinae classification (*e.g.*, LeConte 1856; Harold 1869) attempted to place some Nearctic genera near Palaearctic taxa, and seemed reluctant to erect new tribes for several of the more enigmatic or problematic groups. The catalog of Dalla Torre (1912, 1913) exacerbated the problem by combining taxa from disparate faunas into tribes established primarily for the Palaearctic fauna, an unfortunate taxonomic legacy that continues to hamper efforts to better understand the classification of the Melolonthinae. Evans (2002) provided the most recent synopsis on the Nearctic melolonthines, while Evans & Smith (2009) presented their tribal classification within the context of the New World fauna. The present study represents the culmination of our ongoing investigations into the tribal placement of those Nearctic genera previously considered *incertae sedis*, including *Acoma* Casey, 1889, *Chaunocolus* Saylor, 1937, *Chnaunanthus* Burmeister, 1844, and the former Tanyproctini genera *Phobetus* LeConte, 1856 and *Warwickia* Smith & Evans, 2005.

Recent phylogenetic studies on Melolonthinae have not dealt definitively with any of the Nearctic taxa above. Browne & Scholtz (1998) included *Acoma* and *Chnaunanthus* in their phylogenetic analysis of Scarabaeidae using hindwing articulation characters but reported that these two genera were in a clade with the other Melolonthinae without elaborating on any specific details. Sanmartin & Martín-Piera (2003) conducted a phylogenetic analysis of the Palaearctic Tanyproctini (as Pachydemini) and found that *Phobetus* was the sister taxon to the small region set of Tanyproctini species they investigated. However, the taxon sampling of their study was limited and provided no insights as to where *Phobetus* should be placed. Ahrens (2006) used *Acoma* in his morphological phylogeny

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of Sericini and found that it came out in a clade with some Chasmatopterini, Pachypodini, and Tanyproctini taxa. However, the taxon sampling across Melolonthinae was not broad enough taxonomically or geographically to place *Acoma* within any tribe (*e.g.*, no other Nearctic Melolonthinae were in the analysis). Some African and Palaearctic Tanyproctini genera were the subject of a recent molecular phylogenetics study (Eberle *et al*. 2019) and we agree with their findings that the tribe is a paraphyletic conglomeration of several lineages. Unfortunately, Eberle *et al*. (2019) did not include any New World Tanyproctini so their study provided no insights into the Nearctic genera, either. Other recent molecular phylogenetics results (*e.g.*, Ahrens *et al*. 2014; Gunter *et al*. 2016) have provided a preliminary framework for Melolonthinae but still lack numerous key taxa and provide no insights into the Nearctic genera reclassified in this work.

The main purpose of this paper is to provide an identification key to the Melolonthinae tribes of the Nearctic and to describe four new tribes of Nearctic Melolonthinae in order to appropriately classify some chronically problematic genera. We also take the opportunity to describe four new species of *Acoma* and make some needed adjustments to Melolonthinae tribal classification. In light of the recent tribal classification of the Palaearctic melolonthine fauna (see Löbl & Löbl 2016) and phylogenetic investigations of *Phyllophaga* Harris, 1827 *sensu lato* (Coca-Abia 2007; Rivera-Gasperín & Morón 2013, 2017a, 2017b), we also re-examine the generic composition of the Nearctic Melolonthini and Rhizotrogini. This will properly align the classification of these tribes between the Nearctic and Palaearctic.

Materials and methods

Specimens. Specimens were examined from or deposited in the following entomology collections (with curator/collection manager in parentheses):

AVEC	Arthur V. Evans Collection, Richmond, Virginia, United States of America
CASC	California Academy of Sciences, San Francisco, California, United States of America (Christopher Grinter)
CMNC	Canadian Museum of Nature, Ottawa, Ontario, Canada (François Geìnier, Robert Anderson)
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, United States of America (Wieping Xie, Brian Brown)
SDMC	San Diego Museum of Natural History, San Diego, California, United States of America (Michael Wall)
UNAM	National Insect Collections, Universidad Nacional Autónoma de México, México, Distrito Federal, México (Santiago Zaragoza-Caballero)

Label data and specimen images. The verbatim label data is given for specimens in quotation marks with a single slash "/" to indicate a new line of text on the label and a double slash "//" to indicate a new label. The specimen images were taken at the Canadian Museum of Nature using a Leica DFC495 camera, Leica Z16 APO A microscope, and associated equipment and the Leica Application Suite version 4.2 software. The specimen images were modified and plates constructed in Adobe Photoshop (www.photoshop.com).

Subfamily Melolonthinae

Our diagnosis of the Melolonthinae below is based largely on Evans (2002).

Diagnosis. Scarabaeidae. Adults 3–60 mm in length. Dorsal surface glabrous, setose or scaled; sometimes setae or scales forming distinct patches or lines; color testaceous to reddish brown or black, occasionally with metallic blue, green, coppery, or brassy luster. Head usually unarmed, never with frontal extensions or horns. Eyes only partially divided by ocular canthus. Antennae with 7–10 antennomeres, rarely more, and insertions not visible from above; lamellate club usually consisting of 3–7 antennomeres; lamellae glabrous or with only a few setae, often longer in males. Mandibles sclerotized, usually well developed, and concealed in dorsal view. Transverse, narrowed, or conical labrum free or fused beneath clypeus, sometimes extending beyond or fused to apical clypeal margin. Thorax with pronotal disc more-or-less convex, never concave or with raised carinae; scutellum exposed. Elytra with lateral margins more-or-less straight behind humerus, with mesepimeron usually covered by elytral bases. Metathoracic wings fully developed or reduced. Metepimeron rectangular or triangular. Legs with procoxae transverse or conical; protibiae usually with apical spurs; mesotibiae and metatibiae usually with a pair of apical spurs located below or set on either side of tarsal articulation, or with upper spur adjacent to tarsal articulation; opposing mesotarsal and metatarsal claws equal in thickness (except *Hoplia*, which have a single, enlarged metatarsal claw; see comments below on female *Acoma*) and length and simple, cleft, bifid, toothed, or pectinate. Abdomen often concave medially in males, flat or slightly convex in females; sternites imbricate or smooth, narrowed medially or not, with sutures visible or completely effaced medially; sternite and propygidium fused or not with or without trace of suture; sixth sternite partially or completely retracted beneath fifth; pygidium exposed; 7 or fewer pairs of abdominal spiracles scarcely or not divergent posteriorly, with 1–3 posterior abdominal spiracles located in sternites or tergites. Male genitalia without sclerotized median lobe.

TABLE 1. Extant tribes of Melolonthinae and their distribution (see Bouchard *et al*. 2011; Löbl & Löbl 2016; Smith & Evans 2018; and the new tribes proposed in this paper).

Tribe	Distribution
Ablaberini Blanchard, 1850	Afrotropical
Acomini Evans & Smith, **new tribe**	Nearctic
Athliini Smith & Evans, 2018	Neotropical
Automoliini Britton, 1978	Australian
Chasmatopterini Lacordaire, 1855	Palaearctic
Chnaunanthini Evans & Smith, **new tribe**	Nearctic
Colymbomorphini Blanchard, 1850	Australian
Comophorinini Britton, 1957	Australian
Dichelonychini Burmeister, 1855	Nearctic
Diphucephalini Laporte, 1840	Australian
Diphycerini Medvedev, 1952	Oriental, Palaearctic
Diplotaxini Kirby, 1837	Afrotropical, Nearctic, Neotropical, Oriental
Euchirini Hope, 1840	Oriental, Palaearctic
Heptophyllini Medvedev, 1951	Oriental, Palaearctic
Heteronychini Lacordaire, 1855	Australian
Hopliini Latreille, 1829	Afrotropical, Nearctic, Neotropical, Oriental, Palaearctic
Leucopholini Burmeister, 1855	Australian, Oriental, Palaearctic
Lichniini Burmeister, 1844	Neotropical
Liparetrini Burmeister, 1855	Australian
Macrodactylini Kirby, 1837	Nearctic, Neotropical, Oriental
Maechidiini Burmeister, 1855	Australian, Oriental
Melolonthini Leach, 1819	Afrotropical, Nearctic, Neotropical, Oriental, Palaearctic
Pachypodini Erichson, 1840	Palaearctic
Pachytrichini Burmeister, 1855	Australian
Phobetusini Evans & Smith, **new tribe**	Nearctic
Phyllotocidiini Britton, 1957	Australian
Rhizotrogini Burmeister, 1855	Nearctic, Neotropical, Oriental, Palaearctic
Scitalini Britton, 1957	Australian
Sericini Kirby, 1837	Afrotropical, Nearctic, Palaearctic, Oriental
Sericoidini Erichson, 1847	Neotropical
Schizonychini Burmeister, 1855	Afrotropical, Oriental, Palaearctic
Systellopini Sharp, 1877	Australian
Tanyproctini Erichson, 1847	Afrotropical, Neotropical, Oriental, Palaearctic
Warwickiini Evans & Smith, **new tribe**	Nearctic

Evans & Smith (2009) considered the Nearctic genera *Acoma*, *Chaunocolus*, and *Chnaunanthus* as *incertae sedis*, while following the traditional placement of both *Phobetus* and *Warwickia* in tribe Tanyproctini. The tribal placement of all these genera is reconsidered below. During the course of our investigations, all worldwide Melolonthinae tribes (see Table 1 for a complete list) were studied and we found no compelling morphological characters indicating that *Acoma*, *Chaunocolus*, *Chnaunanthus*, *Phobetus*, or *Warwickia* belong to any of them.

Excluded taxa. Oncerinae new status and Podolasiinae new status. Evans (2002, 2003), Smith (2006), and Bouchard *et al*. (2011) all considered Oncerini and Podolasiini as tribes within the Melolonthinae. With regards to Oncerini, we now follow Saylor (1938), who considered both *Oncerus* LeConte, 1856 and *Nefoncerus* Saylor, 1938 in the subfamily Oncerinae on the basis of the placement of all abdominal spiracles within the pleural membrane. Ritcher (1969) confirmed Saylor's findings for the placement of abdominal spiracles in *Oncerus*, but apparently did not examine the more rarely collected *Nefoncerus*. In addition to the placement of their abdominal spiracles, both of these monotypic genera are characterized by having hidden mandibles, labrum fused and coplanar with the clypeus, small and moderately setose lamellate clubs, and abdominal sutures that are distinct or not.

Howden (1997) erected the tribe Podolasiini for *Podolasia* Harold, 1869 and his new genus, *Podostena* Howden, 1997, and stated that its position within the Melolonthinae is "problematical" and "remains debatable since some characters are not typical for the subfamily". Ritcher (1969) found *Podolasia* to have seven pairs of functional spiracles and a vestigial eighth pair, all located in the pleural membrane. Lacroix (2007) considered the Podolasiinae (Podolasiini), along with the Palaearctic Chasmatopterinae (Chasmatopterini) to be in the Chasmatopteridae without discussion or justification. As mentioned previously, this presumed relationship is untenable given that *Chasmatopterus* Dejean, 1821 and *Podolasia* have very different abdominal spiracle configurations. The lack of any posterior abdominal spiracles in the tergites or sternites, and the small, nearly globose, and densely setose lamellate antennal clubs, combined with the cephalic armature and genital capsule characters found in recently described *Podolasia* (see Smith & Paulsen 2017), and an undescribed *Podostena* species (Evans, personal observation) from Mexico precludes the inclusion of Podolasiini within the Melolothinae, thus requiring its elevation to the subfamily rank of Podolasiinae. The phylogenetic position of this new subfamily with relation to the Melolonthinae needs further study and it will likely occupy a branch basal to the phytophagous scarab clade (see Smith *et al*. 2006).

Tribe Acomini Evans & Smith, new tribe

Figs. 1–28.
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Type genus. *Acoma* Casey, 1889.

Description. Melolonthinae. Head with supraorbital carina. Clypeal suture evident only at lateral margins. Ocular canthus present, not continuous with supraocular carina. Antennae with 9 or 10 antennomeres, club with 3–6 antennomeres. Labrum narrow, greatly reduced, located below and fused to clypeus, clypeolabral suture evident or not. Mandibles reduced. Mentum narrow and flat with ligula distinct. Pronotum with anterior margin narrowly membranous. Elytra elongate-oval in outline, widest at middle, weakly to moderately punctostriate, covering part (female) or all of propygidium (male), metepimeron not evident. Metathoracic wings present (male) or absent (female). Metepisternum elongate. Abdomen with 6 distinct sternites with sutures evident, each with a narrow membranous posterior margin, sternites 2–5 slightly narrowed medially, 5 longest, 6 mostly withdrawn beneath 5; fifth abdominal sternite and propygidium separated by propygidial-sternal suture, spiracle not evident in or near suture. Prothoracic legs with conical and protuberant coxae; tibia bidentate or tridentate, with apical spur. Mesotibiae and metatibiae each with complete medial transverse carinae, apices with 2 apical spurs. Metatibial apex oblique, abruptly expanded, with inner margin broadly notched, corbel with distinct carina around base of tarsal articulation ending above in a short, triangular process beside base of tarsomere, apical spurs set apart with one below and one beside tarsal articulation. Metafemora globose. Opposing claws equal, simple, in between with short, bisetose onychium between them; apparently one metatarsal claw in female (based on the one known female specimen, which only has one intact metatarsus).

Sexual dimorphism. Based on *Acoma knulli* Howden, 1958 using the only known female specimen (Figs. 1–4) for the tribe (from the CMNC labeled "13 Mi.N.E. Rodeo / Hidalgo Co., N.M. / VII-6-1964 // Collectors / Jean H. Puckle / M. A. Mortenson / M. A. Cazier") and 35 male specimens from the same general vicinity. Dorsal color dark brown in males (light brown in the female); antennal club at least 1.5 times longer than funicle and scape in males (distinctly shorter than funicle and scape in the female); eyes large, extending approximately half the length of the head, bulbous when viewed ventrally in males (reduced to a flat strip of ommatidia limited to approximately one-eighth the length of the head in the female; Figs. 2–3); elytra covering the entire abdomen when viewed dorsally in males (distinctly shorter than abdomen in the female); wings fully developed in males (absent in females); tarsi distinctly longer than tibiae in males (shorter than tibiae with reduced claws in the female; Figs. 1–4); metatarsi with small unguitractor plate bearing two setae between the claws in males (unguitractor plate absent and only a single, reduced metatarsal claw in the female); abdomen slightly concave when viewed laterally in males (convex in the female; Fig. 4).

Diagnosis. The placement of the labrum below the clypeus in *Acoma* excludes its inclusion in the Athliini, Sericini, and Sericoidini. In addition to *Acoma*, the Nearctic *Fossocarus* Howden, 1961, *Gronocarus* Schaeffer, 1927 (tribe Rhizotrogini, see below), and a few *Diplotaxis* Kirby, 1837 (Diplotaxini) also have simple claws. *Acoma* is readily distinguished from all of these taxa by having a small labium with a free ligula, glabrous or nearly glabrous head and pronotum, long and nearly glabrous antennal club, broadly rounded posterior pronotal angles, and metathoracic legs with globose femora and distally expanded tibia, corbels, and long tarsi. Further, the propygidium of *Diplotaxis* and other Diplotaxini is completely fused to the fifth sternite.

The Neotropical Tanyproctini genera *Anahi* Martínez, 1958 and *Puelchesia* Ocampo & Smith, 2006 and the subgenus *Acylochilus* (*Acylochoides*) Martínez, 1975 all have simple claws and many similar modifications to the mouthparts and legs as seen in *Acoma*, presumably as an adaptation to desert habitats. *Acoma* is distinguished from *Acylochilus* Ohaus, 1909 and *Puelchesia* by having 9–10 antennomeres (*Acylochilus* and *Puelchesia* have 8 antennomeres) and from *Anahi* by having the metatibiae moderately elongate with apex approximately 2 times as wide as the base (*Anahi* has the metatibiae apex 5 times wider than the base and cone shaped).

Composition. Acomini **new tribe** is represented solely by *Acoma* Casey, 1889.

Habitat and distribution. *Acoma* is restricted to the Nearctic realm in warm Chihuahuan and Sonoran Deserts, and thorn-scrub habitats (southeastern California to western Texas in the United States of America, south to Baja California Sur, northwestern Sonora, and Chihuahua in Mexico).

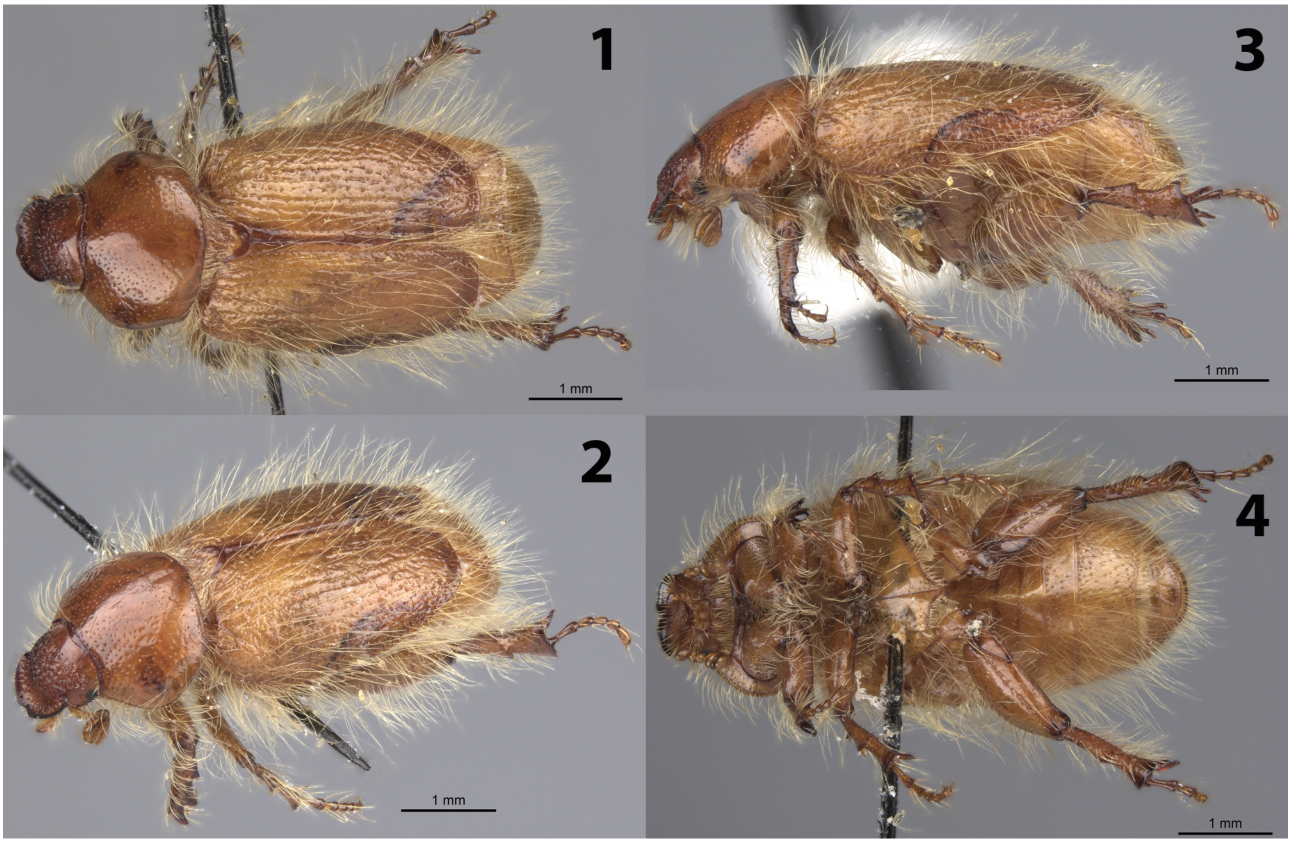
Habits. Casey (1890) erroneously suggested that *A. brunnea* Casey, 1889 probably lived in flowers or on plants, and noted that he had not seen any females. Van Dyke (1928) was the first to report the attraction of male *Acoma* to light and, due to the lack of specimens, speculated "...that the females are either wingless or are very limited in their activities..." Male *Acoma* become active at dusk, are attracted to light on hot evenings just after dark in late spring and summer, where they typically remain only briefly; some individuals will take refuge beneath light sheets. Populations usually occur along the edges of washes that are vegetated with mesquite and are not prone to flooding and form large drainage systems that cross sand dunes or flat habitats with alluvial soils (Howden 1962, 1963; Warner 2011). Extensive digging during the day under mesquite trees, in grassy clumps, and along wash banks by Howden (1962) yielded no beetles or larvae, nor did attempts to find males emerging from the soil in the early evening. However, a single female of *A. knulli* (Figs. 1–4) was excavated from a sandy flat near Rodeo, New Mexico by about 20 students working under the direction of Mont Cazier (Warner 2011; Howden *et al*. 2014).

Remarks. Casey (1890) placed *Acoma* near *Podolasia*, thus allying it with *Chnaunanthus* and *Oncerus* in the tribe Oncerini (Melolonthinae). Later, Arrow (1912) positioned *Acoma* next to *Pleocoma* LeConte, 1856 within the Pleocominae without explanation, while *Chnaunanthus*, *Oncerus*, and *Podolasia* were placed in the Chasmatopterini (Dalla Torre 1912). Leng (1920) followed both of these classifications. Van Dyke (1928), noting the paucity of females in collections, suggested their possible flightless condition and considered the genus to be related to *Pleocoma*. After examining both its mouthparts and placement of the abdominal spiracles, Davis (1934) disputed the inclusion of *Acoma* in the Pleocominae. He observed that *Pleocoma* clearly did not share abdominal spiracle characters with the phytophagous scarab groups, while *Acoma* did have these shared characters and thus he allied the latter with *Podolasia*. Saylor (1937a) also suggested that *Podolasia* was likely the nearest relative of *Acoma*. Blackwelder (1944) placed *Acoma* in the melolonthine tribe Chasmatopterini, along with *Chnaunanthus* and *Chaunocolus*, but Cazier (1953) and Arnett (1962) retained it within the Pleocominae. Howden (1958) noted that the phylogenetic placement of *Acoma* would remain in doubt until more information became available on the morphology of the unknown female.

In his study on abdominal spiracle placement in the Scarabaeoidea, Ritcher (1969) examined specimens of *Acoma* and found functional spiracles corresponding with segments 1–5, all of which are situated in the pleural membrane. Spiracles associated with abdominal segments 6–8 are vestigial. Of these, both 6 and 8 located in the pleural membrane, spiracles associated with segment 7 are located in the sternite. In his consideration of the tribal placement of *Warwickia* (as *Benedictia* Sanderson, 1939, see Smith & Evans 2005), Hardy (1978a) considered *Acoma* to be a melolonthine and removed it from the Pleocominae. Browne & Scholtz (1998) observed that *Acoma* does not display any autapomorphic hindwing articulation or wing base character state, but does share two apomorphic character states of the wing articulation with Melolonthinae, *Chnaunanthus*, *Oncerus*, and Hopliini, suggesting that these taxa together form a monophyletic group. A phylogenetic analysis of Sericini (Ahrens 2006) revealed six major clades with the Scarabaeidae and placed *Acoma* within "melolonthine group I, node D" that did not hypothesize any tribal affinities. Recent overviews of the New World melolonthine fauna (Evans 2002, 2003; Evans & Smith 2009; Smith & Evans 2005) have considered *Acoma* as *incertae sedis* within Melolonthinae.

Our examination of the single known female specimen of *Acoma* (Figs. 1–4) confirms that the characters of male *Acoma* alone are sufficient for placing *Acoma* as the sole genus in a new tribe within the Melolonthinae.

While identifying miscellaneous melolonthines at the Canadian Museum of Nature and California Academy of Sciences, we discovered unidentified specimens of *Acoma* that did not fit in the key provided in Warner (2011). Subsequent comparison of these specimens with many holotypes and paratypes revealed the four new species described below.



FIGURES 1–4. *Acoma knulli* Howden, 1958 female. **1**, Dorsal habitus; **2**, oblique habitus; **3**, lateral habitus; **4**, ventral habitus.

Acoma chihuahuaensis Evans & Smith, new species

Figs. 5–10

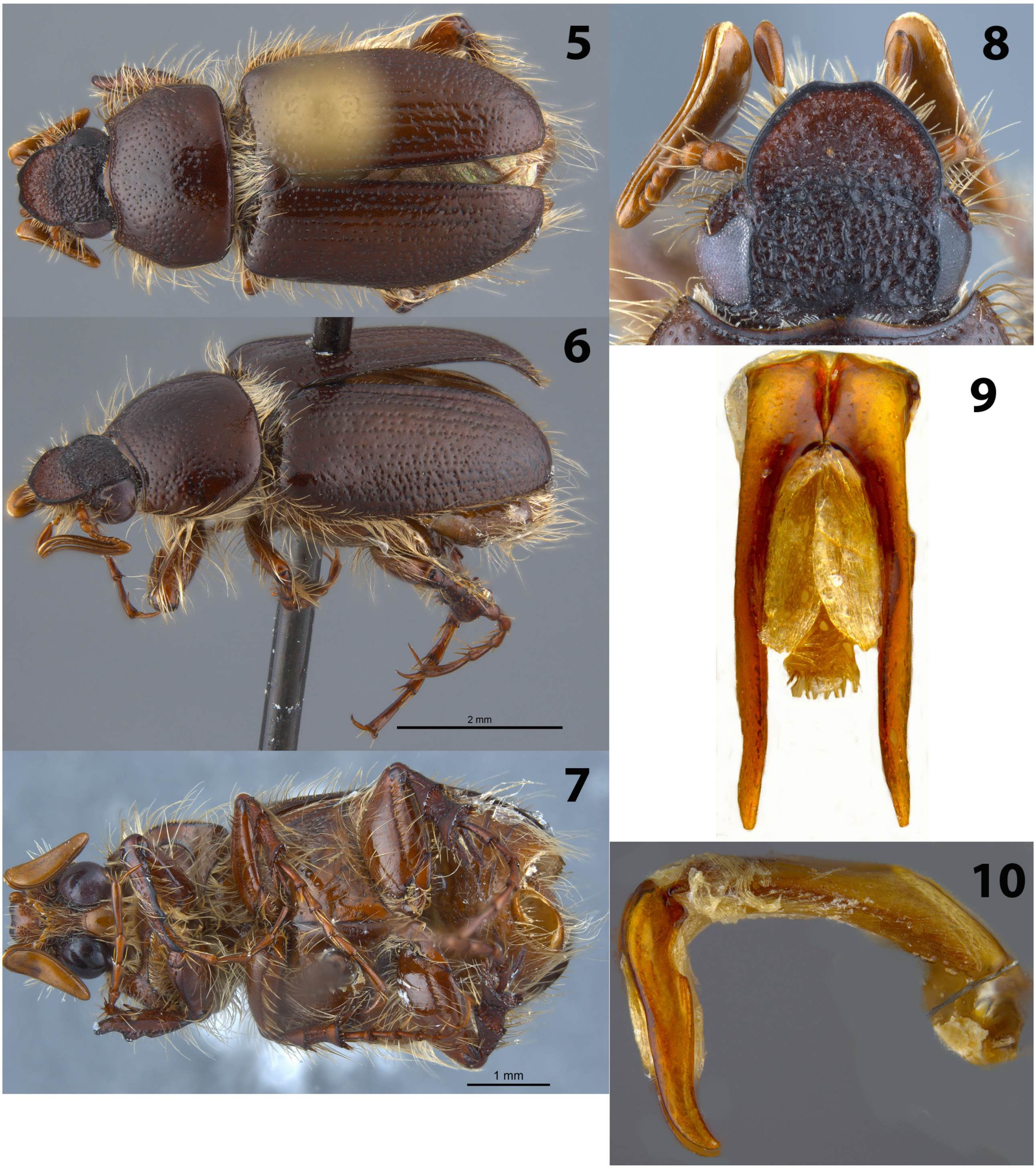
urn:lsid:zoobank.org:act:BD4FB72A-5BD1-4671-886A-C0E05D1BE391

Type material. Holotype male (CASC Type 19747), labeled "MEXICO: Chihuahua / 7.1 mi. W Concho / VII-23-1982 / Fred G. Andrews / coll. blacklight // Dr. Alan R. Hardy / Donation to the / California Academy / of Sciences // CASENT / 8424526 // HOLOTYPE / Acoma / chihuahuaensis / Evans & Smith, 2019".

Paratypes, (9 males): same data as holotype, except with CASC database numbers CASENT 8424527–8424535.

Paratypes are deposited in AVEC (1 paratype; CASENT 8424534), CASC (6 paratypes; CASENT 8424527–8424532), CMNC (1 paratype; CASENT 8424535), UNAM (1 paratype; CASENT 8424533).

Diagnosis. Brown dorsally; anterior clypeal margin emarginate medially; antennae composed of 10 antennomeres, antennomeres 8–10 lamellate; protibia distinctly tridentate; elytra with disc glabrous and scattered setae along margins.



FIGURES 5–10. *Acoma chihuahuaensis* Evans & Smith, new species, male holotype. **5**, Dorsal habitus; **6**, oblique habitus; **7**, ventral habitus; **8**, head; **9**, dorsal parameres; **10**, lateral genitalia.

Description. Holotype male (Figs. 5–10), length: 6.9 mm, width: 2.6 mm. BODY elongate, moderately convex, and uniformly brown dorsally, underside and appendages slightly lighter. HEAD (Fig. 8) rugosely punctate; supraorbital carinae becoming obsolete at base of clypeus. Clypeus subtrapezoidal with margins strongly reflexed, lateral margins arcuate basally, becoming straight before broadly concave anterior margin flanked by prominent obtuse angles. Ocular canthus slightly less than one-third of eye length in lateral view, with scattered pale setae each not quite as long as canthus. PRONOTUM slightly wider than long, broadest at middle, and less than half length of elytron; disc convex, glabrous, shiny, sparsely punctate with punctures separated by four or more of their diameters, with a narrow longitudinal impunctate line medially; margins with distinct bead, anterior margin bisinuate between obtuse anterior angles, with marginal bead relatively broad and raised; anterolateral margins straight, converging anteriorly, posterolateral margins slightly converging posteriorly with posterolateral angles broadly rounded. SCUTELLUM small, parabolic, about one-fifth basal width of elytron, finely and setigerously punctate basally, and glabrous and becoming impunctate apically. ELYTRON convex, with disc shiny, glabrous, and distinctly punctostriate with deep punctures separated by 1.5–3.0 X their diameters, punctures becoming confused at apical declivity; margins setigerous, setae on lateral margins becoming shorter apically. LEGS with tridentate protibia moderately emarginate between apical and middle teeth, and shallowly emarginate between middle and basal teeth. PYGIDIUM parabolic, shiny, finely shagreened, with scattered setigerous punctures, setae long. GENITALIA with parameres symmetrical, slender and slightly sinuate when viewed laterally, with membranous flange extending to apical fifth, and about as long as phallobasis (Figs. 9–10).

Variation. Length: 5.9–6.9 mm, width: 2.2–2.6 mm. Color varies from light brown to brown, occasionally with elytra lighter, while the head and pronotum are slightly darker. Clypeus varies from subtrapezoidal to nearly parabolic with narrowly to broadly concave anterior margin flanked by prominent angles or not.

Etymology. This species is named after the Mexican state of Chihuahua, where the type series was collected.

Remarks. *Acoma glabrata* Cazier, 1953, *A. nonglabrata* **new species**, and *A. chihuahuaensis* **new species** all have antennae with 10 antennomeres, of which 8–10 form the lamellate club. *Acoma chihuahuaensis* **new species** is readily distinguished among these species by its darker color, distinct elytral punctostriae with deep punctures, more rounded and less pronounced protibial teeth, and its occurrence in mainland Mexico.

Acoma eusexfoliata Evans & Smith, new species

Figs. 11–16

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Type material. Holotype male (CASTYPE 19860), labeled "MEXICO, Baja Calif. Norte / 2 mi. SW San Francisquito / box canyon with caves BL / VII-26/27-86 R. L. Aalbu // Dr. Alan Hardy / Donation to the / California Academy / of Sciences // CASENT / 8424551 // HOLOTYPE / Acoma / eusexfoliata / Evans & Smith, 2019".

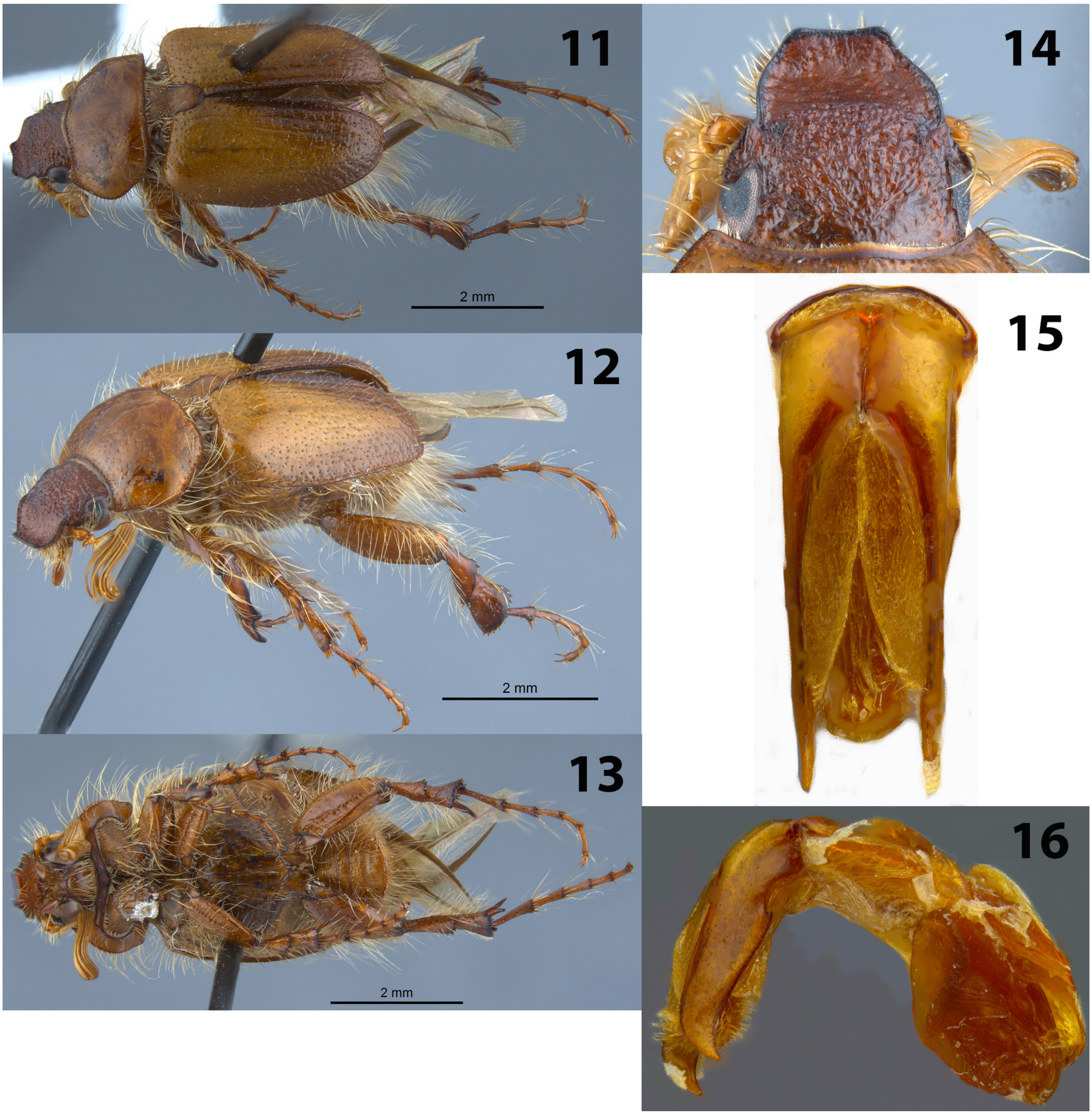
Diagnosis. Light reddish testaceous dorsally with head and pronotum darker; anterior clypeal margin weakly emarginate and strongly reflexed; antennae composed of 9 antennomeres, antennomere 3 much longer than 1+2 with anterior projection at base, 4–9 lamellate; protibia apparently bidentate; elytral disc with scattered erect setae.

Description. Holotype male (Figs. 11–16), length: 6.0 mm, width: 4.0 mm. BODY somewhat robust, testaceous, with head, pronotum and elytral apices slightly darker. HEAD (Fig. 14) with vertex rugosely punctuate, clypeus shagreened with large shallow punctures separated by their own diameters or more; supraorbital carinae becoming obsolete at bases of head and clypeus. Clypeus subtrapezoidal with lateral margins broadly arcuate and weakly reflexed; anterior margin shallowly concave, not quite truncate, strongly reflexed, and angulate. Ocular canthus about one-quarter of eye length when viewed from side, with scattered pale setae each longer than canthus. PRONOTUM wider than long, broadest before middle, slightly more than one-third length of elytron; disc strongly convex, sparsely and shallowly punctate, with broad impunctate area medially; lateral and posterior margins with bead; anterior margin broadly concave between obtuse anterior angles; anterolateral margins straight and convergent anteriorly, posterolateral margins slightly concave and convergent posteriorly, with posterior angles broadly rounded. SCUTELLUM broadly parabolic, about one-quarter width of elytron, setigerously punctate at base, finely shagreened medially and apically. ELYTRON convex, shiny, finely shagreened, disc punctostriate with punctures becoming confused on apical and lateral declivities, setigerous punctures with short, suberect setae. LEGS with protibial apparently bidentate, basal third tooth barely indicated by weak angulation. PYGIDIUM parabolic, finely shagreened, with scattered setigerous punctures, setae long. GENITALIA with parameres symmetrical, moderately slender and more or less straight when viewed laterally, with membranous flange extending to apical 3/5, and shorter than phallobasis (Figs. 15–16).

Variation. This species is known only from the holotype.

Etymology. This species is named for actually having 6 antennomeres in its antennal club, unlike *A. sexfoliata* Saylor, 1948, which has 7 antennomeres.

Remarks. *Acoma eusexfoliata* **new species** is distinguished from all other known *Acoma* species by its antennal configuration. The unique holotype was originally glued by its abdomen to a point. The specimen was placed in hot water and removed from the point and pinned. While removing the abdomen for genitalic dissection, the right protibia was accidentally detached the body at the base of the femur. Rather than gluing the detached appendage back in place, it was affixed intact onto a separate point and pinned below the specimen.



FIGURES 11–16. *Acoma eusexfoliata* Evans & Smith, new species, male holotype. **11**, Dorsal habitus; **12**, oblique habitus; **13**, ventral habitus; **14**, head; **15**, dorsal parameres; **16**, lateral genitalia.

Acoma nonglabrata Evans & Smith, new species

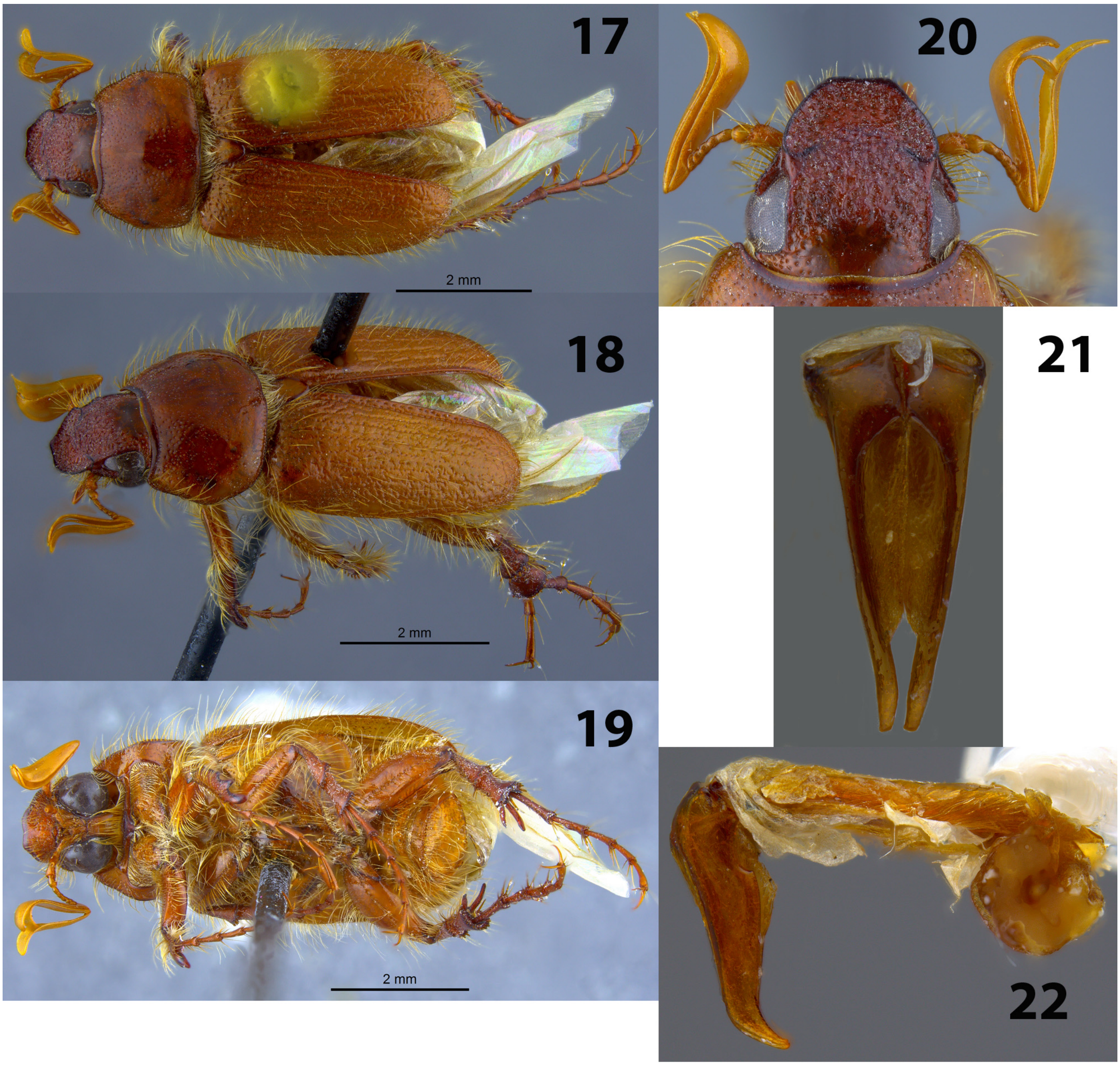
Figs. 17–22
urn:lsid:zoobank.org:act:8EBF5164-E12F-4C2B-BE80-21ACF3429289

Type material. Holotype male (CASCTYPE 19748), labeled "MEXICO: BajaCal. Norte / Guadalupe Canyon, E. / side of SierraJuarez / 18-VI-1973 S.C. / Williams & K.B. Blair / SCW # 311 (2) // ACOMA / OCHLERA / HOWDEN / OR N.SP. NEAR / det.W.B.Warner 2015 // CASENT / 8424501 // HOLOTYPE / Acoma / nonglabrata / Evans & Smith, 2019".

Paratypes (7 males): 5, same data as holotype, except no determination label, CASC database numbers CASENT 8424502–8424506; 2, "MEX. BajaCalif.Norte / 5.3km S Bajia de Los / Angeles VII.9–10.78 / 59029.6 / E. L. Sleeper" (CMNC) and "BCN-5.3 km S / BAJIA DE LOS / ANGELES / VII-9/10-1978 // 59029.6 / E. L. Sleeper" (CMNC).

Paratypes are deposited in AVEC (1 paratype; CASENT 8424502), CASC (2 paratypes; CASENT 8424505–8424506), CMNC (1 paratype; CASENT 8424503), UNAM (1 paratype; CASENT 8424504).

Diagnosis. Light reddish tan dorsally with head and pronotum darker; anterior clypeal margin emarginate medially; antennae composed of 10 antennomeres, antennomeres 8–10 lamellate; protibia distinctly tridentate; elytral disc with scattered setae.



FIGURES 17–22. *Acoma nonglabrata* Evans & Smith, new species, male holotype. **17**, Dorsal habitus; **18**, oblique habitus; **19**, ventral habitus; **20**, head; **21**, dorsal parameres; **22**, lateral genitalia.

Description. Holotype male (Figs. 17–22), length: 6.5 mm, width: 3.5 mm. BODY testaceous, elongate, moderately convex. HEAD (Fig. 20) with impunctate vertex shiny and slightly depressed, frons and clypeus rugose, clypeus with large shallow punctures evident and separated by their own diameters; supraorbital carina obsolete at base of head and clypeus. Clypeus subtrapezoidal, lateral margins moderately reflexed, anterior margin broadly and shallowly concave with angles not prominent. Ocular canthus about one-quarter length of eye when viewed laterally, setose with setae longer than canthus. PRONOTUM slightly wider than long, broadest medially, convex, about one-third length of elytron; disc convex, glabrous, moderately punctate, most punctures separated by 1–2 diameters, with longitudinal impunctate area medially; lateral and posterior margins with narrow bead; anterior margin moderately bisinuate between obtuse anterior angles, with broad bead; anterolateral margin slightly sinuate and converging anteriorly, posterolateral margin straight and converging slightly posteriorly, with posterior angles broadly angulate. SCUTELLUM parabolic, about one-quarter width of elytron, disc mostly finely shagreened. ELYTRON convex, shiny, finely shagreened, disc punctostriate with punctures becoming confused on apical and lateral declivities, setigerous punctures with long suberect setae. LEGS with tridentate protibia moderately emarginate between teeth. PYGIDIUM parabolic, shiny, finely shagreened, with scattered setigerous punctures, setae long. GENITALIA with parameres symmetrical, slender and slightly sinuate when viewed laterally, with membranous flange extending to apical fourth, and not as long as phallobasis (Figs. 21–22).

Variation. The type series is consistent in length, color, and surface sculpturing, but does exhibit minor variation in the degree of concavity of the anterior clypeal margin and prominence of clypeal angles.

Etymology. This specific epithet is in reference to the superficial resemblance to *A*. *glabrata*, which also occurs in Baja California.

Remarks. With 10 antennomeres and the club consisting of three antennomeres, *A*. *nonglabrata* **new species** superficially resembles *A*. *glabrata*, but is readily distinguished by the setose elytral disc and more angulate lateral pronotal margins.

Acoma pararobusta Evans & Smith, new species

Figs. 23–28

urn:lsid:zoobank.org:act:9342C833-0F57-4CCB-9819-C38902BAE444

Type material. Holotype male (CASTYPE 19749), labeled "MEX.: Baja Calif. Sur / El Sargento, 29.VII. / 1971. At U.V. light / H.G. Real & R.E. Main // **n. sp.**? / DET. / A.R. Hardy 1979 // Acoma / **n. sp.** 3 / det.W.B.Warner 2015 // CASENT / 8424521 // HOLOTYPE / Acoma / pararobusta / Evans & Smith, 2019".

Paratypes, (2 males): same data as holotype, except no determination labels, CASC database numbers CASENT 8424522–8424523.

Paratypes are deposited in CASC (1 paratype; CASENT 8424523), CMNC (1 paratype; CASENT 8424522).

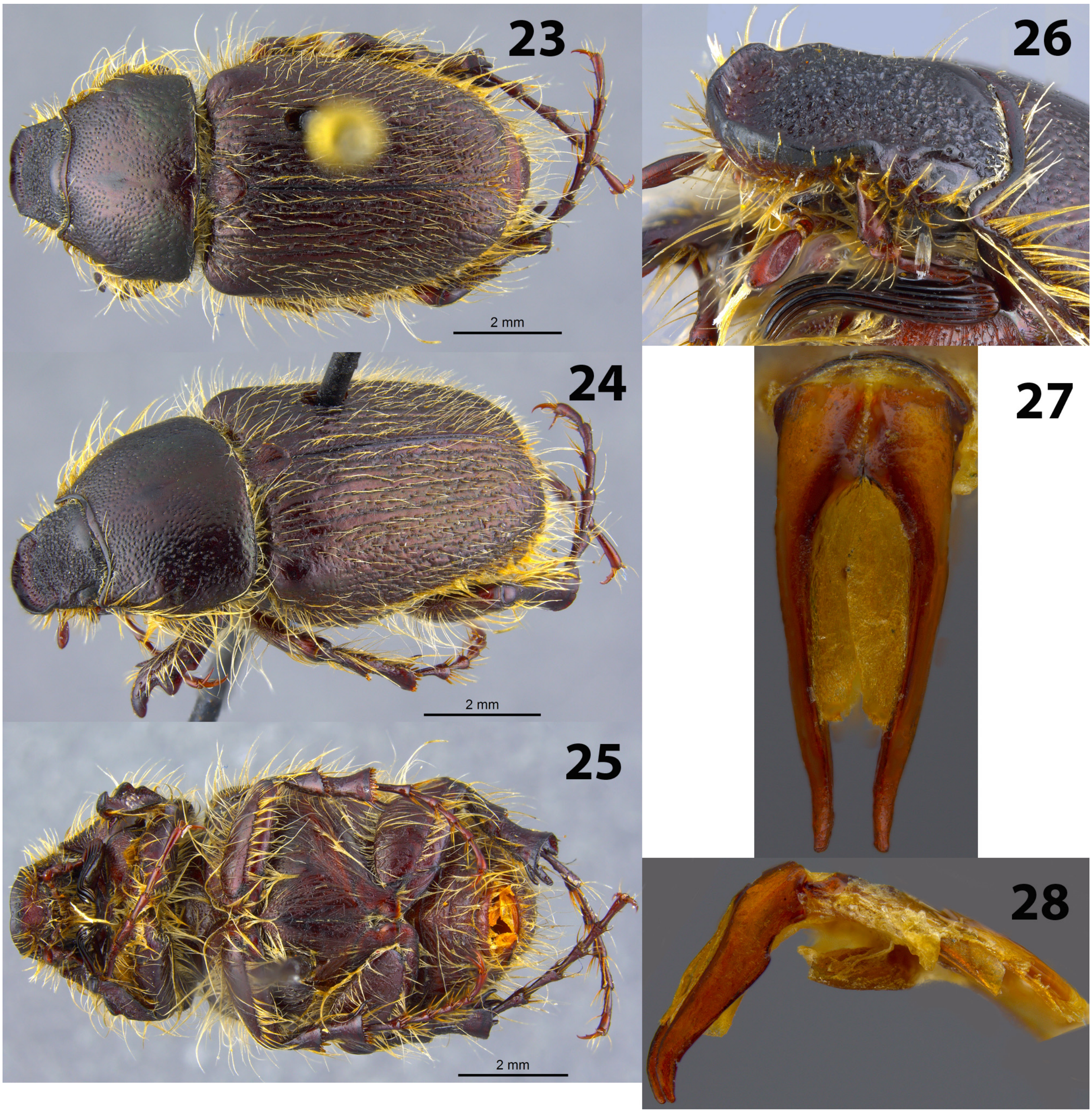
Diagnosis. Rufopiceous or rufobrunneus dorsally; anterior clypeal margin shallowly emarginate or rounded medially; frontoclypeal suture tumid; antennae composed of 9 antennomeres, antennomeres 5–9 lamellate, subequal in length; protibia distinctly tridentate; elytral disc with scattered, pale setae.

Description. Holotype male (Figs. 23–28), length: 9.0 mm, width: 4.0 mm. BODY dark brown, elongate, robust, moderately convex. HEAD (Fig. 26) with narrowly raised transverse impunctate area, frons and base of clypeus deeply and rugosely punctate, reflexed clypeal margins smoother, with deep punctures mostly separated by their own diameters; short and irregular supraorbital carina obsolete at bases of head and clypeus. Clypeus somewhat semicircular, lateral margins narrowly reflexed, apical margin more broadly reflexed and slightly concave. Ocular canthus thick and broadly rounded apically, about one-third length of eye when viewed laterally, densely setose with setae somewhat longer than canthus. PRONOTUM about half length of elytron, as long as wide; disc glabrous with moderately dense punctures usually separated by twice their diameters sometimes briefly confluent on either side of narrow longitudinal impunctate area medially, punctures become denser laterally, even more so anteriorly; anterolateral margins sinuate, abruptly converging anteriorly from middle, posterolateral margins subparallel, shallowly concave medially; lateral and posterior margins with narrow bead, lateral margins distinctly setose with setae long; anterior margin mostly concave between acute and produced anterior angles, slightly protruding medially, with broad bead; posterior angles broadly obtuse. SCUTELLUM broadly elliptical, basal half sparsely and setigerously punctate, setae coarse. ELYTRON shiny and setose, with deep, narrow striae on disc with setigerous punctures bearing recumbent setae becoming short and irregular on declivities. LEGS with tridentate protibia deeply emarginate between apical and middle teeth, shallowly emarginate between middle and basal teeth. PYGIDIUM broadly parabolic, rugosely punctate along sides, and setose with setae long, erect. GENITALIA with parameres symmetrical, slender and slightly sinuate when viewed laterally, with membranous flange extending to apical fourth, and not as long as phallobasis (Figs. 27–28).

Variation. Length: 7.5–9.0 mm, width: 3.2–4.0 mm. Color varies from light to dark brown. Anterior clypeal margin ranges from slightly concave to nearly rounded.

Etymology. This is named in recognition of the similarities with *A. robusta* Van Dyke, 1928.

Remarks. *Acoma pararobusta* **new species** is distinguished from all other species in the genus by the characters given in the diagnosis. In addition to the tumid frontoclypeal suture, it is distinguished from *A. robusta* by the coarse, rugose sculpturing on the frons and base of the clypeus, occasional confluent punctures on pronotal disc, and the somewhat semicircular clypeal margin with bases that are more or less continuous with the supraorbital carinae.



FIGURES 23–28. *Acoma pararobusta* Evans & Smith, new species, male holotype. **23**, Dorsal habitus; **24**, oblique habitus; **25**, ventral habitus; **26**, head; **27**, dorsal parameres; **28**, lateral genitalia.

Tribe Chnaunanthini Evans & Smith, new tribe

Figs. 29–34, 48.

urn:lsid:zoobank.org:act:0C33B7EA-2688-4F7D-8EE8-306CB49D772E

Type genus. *Chnaunanthus* Burmeister, 1844.

Description. Melolonthinae. Antenna with 9 or 10 antennomeres, club with 3 lamellae; transverse labrum fused below clypeus and not extending beyond clypeal margin. Prothorax with membranous anterior pronotal margin. Abdomen with sternites 2–5 subequal in length, slightly narrowed medially, fused with sutures effaced medially, and posterior margin of sternite 5 broadly membranous; sternite and propygidium separated by suture; functional spiracles on segments 1–7, 1–6 in pleural membrane, 7 and vestigial spiracle 8 in tergite (in *Chaunocolus* spiracle 7 appears vestigial and is on the border between the pleural membrane and tergite and spiracle 8 was not found). Legs with procoxae transverse; protibia with apical spur (absent in males), mesotibiae and metatibiae each with pair of apical spurs; metatibial spurs subcontiguous, located below tarsal articulation; opposing tarsal claws similar and bifid or toothed.

Diagnosis. Species of Chnaunanthini are small with reduced mouthparts, and have short oval antennal clubs partly clothed with dense setose surfaces and effaced abdominal sutures. Metatibial spurs both located below the tarsal articulation so that the metatarsomere passes over them; labrum reduced but visible in ventral view of the head, hidden below the clypeus in dorsal view; abdominal sutures entirely effaced ventrally.

Composition. Chnaunanthini **new tribe** consists of *Chaunocolus* Saylor, 1937 (Figs. 32–34) and *Chnaunanthus* Burmeister, 1844 (Figs. 29–31).

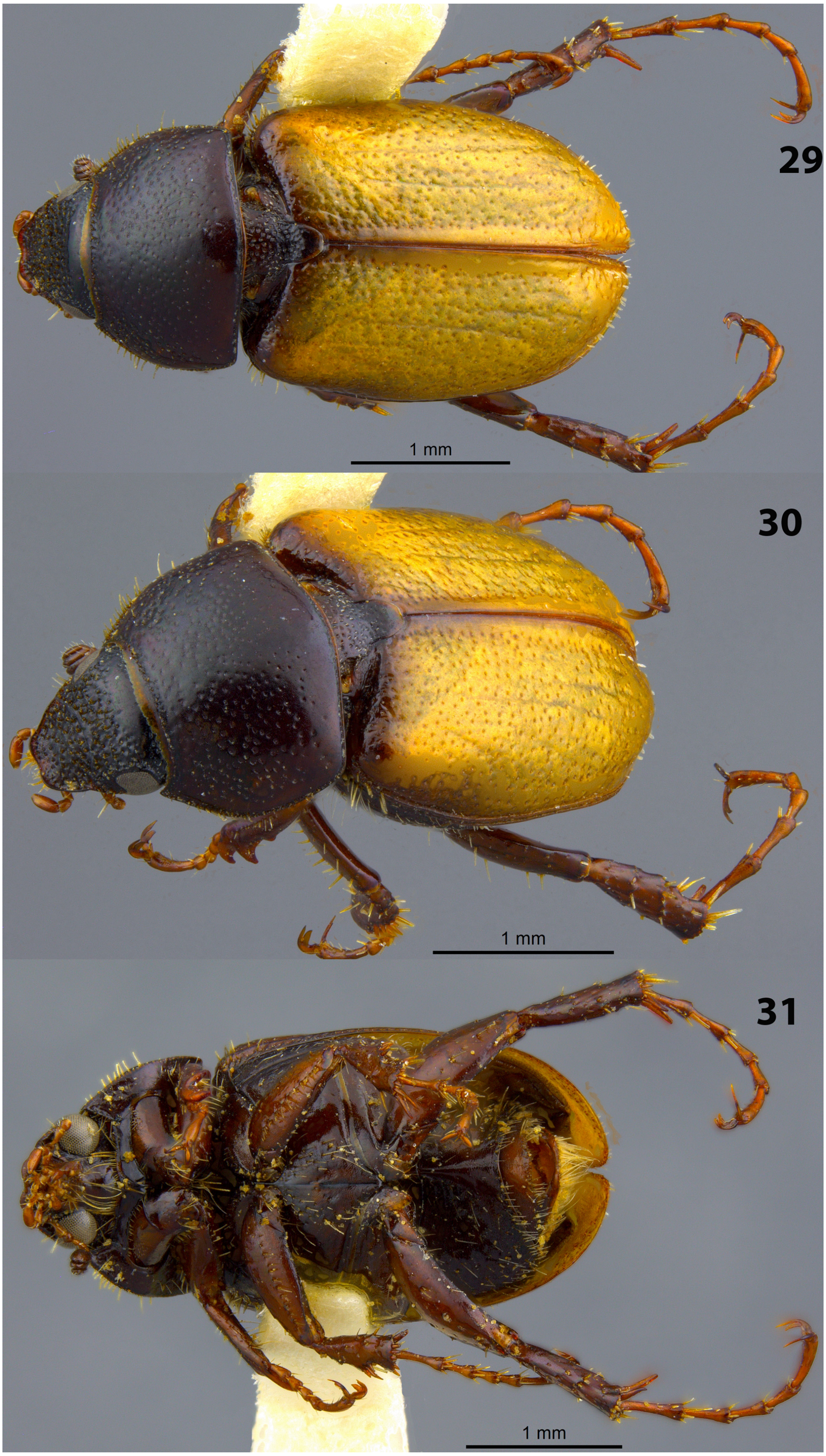
Habitat and distribution. *Chnaunanthus* occurs in the Great Basin, Mojave, and Sonoran Deserts of the Nearctic realm and southward (southeastern Oregon and Utah to southeastern California and southwestern Arizona, and mainland Mexico to Oaxaca, and likely occurs in Baja California Norte (Morón *et al*. 1997; Warner, personal communication). *Chaunocolus cornutus* Saylor, 1937 is endemic to the environs of La Paz, Baja California Sur, Mexico. Label data indicated that specimens of *Chaunocolus cornutus* were collected on *Asclepias* (Apocynaceae) and in pitfall traps on or near the seashore in April, June, and September.

Habits. Adult *Chnaunanthus* are found on desert spring flowers in the United States of America and summer flowers in the southern part of their range in mainland Mexico.

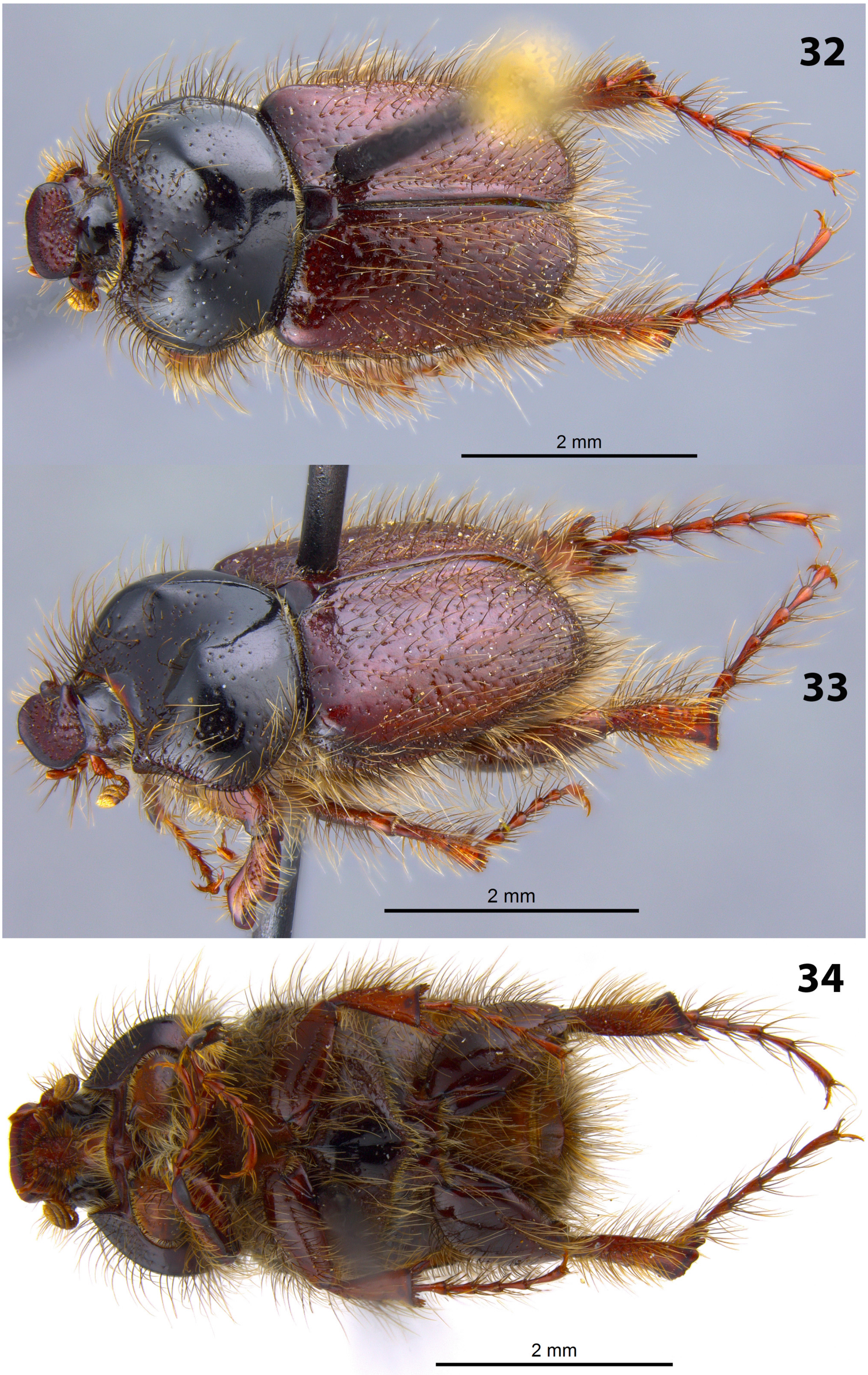
Remarks. *Chnaunanthus* had long been included with the western Palaearctic *Chasmatopterus* in the tribe Chasmatopterini (see Lacordaire 1855; Dalla Torre 1912; Leng 1920, Blackwelder 1944). Saylor (1937a) described a new genus *Chaunocolus* from the Baja California Peninsula and allied it with *Chnaunanthus*, *Oncerus*, and *Podolasia*, but did not include it in his subsequent studies of the Chasmatopterinae (Saylor 1937b) or Oncerinae (Saylor 1938). Arnett (1962) included all of these genera in the Chasmatopterini. In their revision of *Chasmatopterus*, Baraud & Branco (1991) established that this Palaearctic genus was the sole representative of the Chasmatopterinae, an action overlooked in subsequent studies on the New World melolonthine fauna (see Howden 1997; Morón *et al*. 1997; Evans 2002, 2003). Later, Branco (2005) briefly compared the morphology of *Chasmatopterus* with *Chnaunanthus* and *Chaunocolus*, and rightly concluded that the New World genera "belong elsewhere, probably in a subfamily (or tribe) of their own," prompting Smith & Evans (2005) to list both genera as *incertae sedis* and strike the Chasmatopterini from the New World melolonthine fauna. Lacroix (2007) used the name Chnaunanthini, but did not validate it under the International Commission on Zoological Nomenclature (1999). Specifically, Lacroix (2007) did not explicitly indicate "Chnaunanthini" as intentionally new (Article 16.1) and the name is not accompanied by a description or definition or a bibliographic reference to such a published statement (Article 13.1). Lacroix (2007) listed *Chnaunanthus* in the tribe and placed it next to Oncerini within the Oncerinae. This presumed relationship is untenable given the very different abdominal spiracle configurations of *Chnaunanthus* and *Oncerus*.

The cephalic horn and concave pronotum of *Chaunocolus cornutus* are atypical characters within the Melolonthinae and it was difficult to conclusively confirm the placement of abdominal spiracles 7–8 due to their reduction and the very limited number of specimens on hand. Our observation that spiracle 7 appears vestigial and is on the border between the pleural membrane and (subapical) tergite does not entirely correspond with the Saylor (1937a) observation "Propygidium and fifth ventral segments not connate…, the last spiracle very minute and apparently below the suture." His comment does indicate that he did not detect any trace of a spiracle 8 on the pygidium or apical tergite, which corresponds with our observations.

Both genera in this tribe need to be more thoroughly studied to fully determine their relationship within the Melolonthinae.



FIGURES 29–31. *Chnaunanthus discolor* Burmeister, 1844 male. **29**, Dorsal habitus; **30**, oblique habitus; **31**, ventral habitus.



FIGURES 32–34. *Chaunocolus cornutus* Saylor, 1937 male. **32**, Dorsal habitus; **33**, oblique habitus; **34**, ventral habitus.

The Nearctic taxa formerly placed in Tanyproctini

Smith & Evans (2005) provide an overview of the taxonomic history of the tribe Tanyproctini. The name Pachydemini was in stable usage for this taxon until Bouchard *et al*. (2011) resurrected the older, yet unused name Tanyproctini as a senior synonym based on its inadvertent usage as a valid name by Smith (2006). Since 2011, various authors have used either Pachydemini or Tanyproctini (Smith & Mondaca 2016). Lacroix & Montreuil (2014) attempted to conserve the priority of Pachydemini over Tanyproctini using Article 23.9 (International Commission on Zoological Nomenclature 1999), but had overlooked the usage of Tanyproctini as a valid name by Smith (2006), thus nullifying their action under Article 23.9.1.1. The status of these two names now falls under Article 23.10 (erroneous reversal of precedence), which dictates that the matter be referred to the International Commission on Zoological Nomenclature for a ruling. In the meantime, the principle of priority should be applied and the older name (Tanyproctini) be considered as the valid name since neither Tanyproctini nor Pachydemini is in prevailing usage.

More research is needed to determine the phylogenetic relationships of the Neotropical Tanyproctini (see Martínez 1975, 1982). It is unlikely that these genera share any tribal affinities with the Old World Tanyproctini that are distributed primarily in the Palaearctic realm. *Madiniella* Chalumeau & Gruner, 1976, endemic to Martinique, is transferred from Tanyproctini to Rhizotrogini below. As for the remaining two Nearctic tanyproctine genera, Hardy (1978a) suggested that *Warwickia* (as *Benedictia*) shared some similarities with some Neotropical Tanyproctini, but neither it nor *Phobetus* are closely related to any South American genus and they are only distantly related to one another.

Tribe Phobetusini Evans & Smith, new tribe

Figs. 35–37, 52, 57.

urn:lsid:zoobank.org:act:FBED1337-3541-402D-BDE9-EA469CB19DBE

Type genus. *Phobetus* LeConte, 1856.

Description. Melolonthinae. Antenna with 9 or 10 antennomeres, club with 3–6 lamellae. Labrum transverse, free, located below clypeus, and not extending beyond clypeal margin. Prothorax with membranous anterior pronotal margin. Abdomen with sutures distinct, sternites not narrowed medially, 2–4 subequal in length, 5 somewhat or distinctly longer, and posterior margins all membranous; sternite and propygidium separated by suture; functional spiracles on segments 1–7, 1–2 in pleural membrane, 3–7 in sternite. Legs with procoxae transverse; protibia with apical spur, mesotibiae and metatibiae each with pair of apical spurs; metatibial spurs separated, located on each side of tarsal articulation; opposing tarsal claws similar and cleft.

Diagnosis. Phobetusini is distinguished from all other Nearctic melolonthine tribes by the transverse and free labrum located below and not extending beyond the clypeal margin, separated metatibial spurs, membranous anterior pronotal margin, cleft claws, distinct abdominal sutures, and membranous posterior margin of sternites.

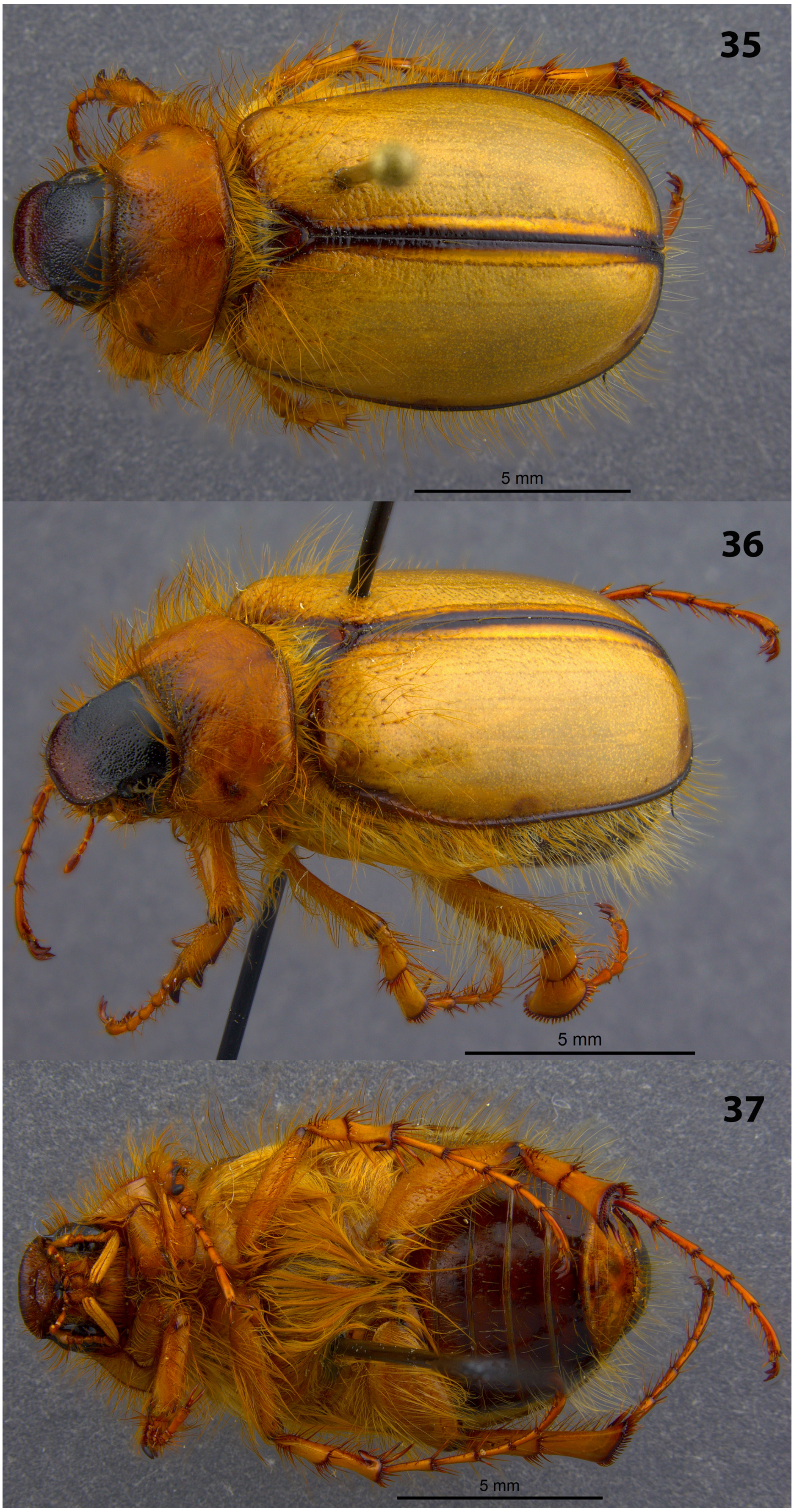
Composition. Phobetusini **new tribe** is represented solely by *Phobetus* LeConte, 1856 (Figs. 35–37).

Habitat and distribution. Species of *Phobetus* are restricted to the Pacific Coast of North America, where they occur in oak and juniper woodlands, coastal chaparral, and portions of the Mojave and Sonoran Deserts (British Columbia, Canada to Baja California Norte, Mexico).

Habits. Adult *Phobetus* are active in late winter and spring. Most are nocturnal and encountered at night feeding and mating on vegetation or attracted to light, but a few species are diurnal or crepuscular and are found flying low over the ground.

Etymology. We have chosen to use the entire generic name *Phobetus*- as the stem for this family-group name (Recommendation 29A) so this spelling of the stem must be maintained under Article 29.4 of the International Commission on Zoological Nomenclature (1999). We have done this to avoid a possible homonym with the name Phobetini / Phobetina (Hymenoptera: Ichneumonidae), which appears in the literature (*e.g.*, Narayanan & Kundanlal 1958; Baltazar 1964). We were unable to determine if the Hymenoptera name was ever made available.

Remarks. Since its description by LeConte (1856), *Phobetus* has been allied with various Afrotropical, Neotropical, and Palaearctic taxa possessing distinct abdominal sutures, which Dalla Torre (1913) had lumped together in the Tanyproctini (as Pachydemini). Lacroix (2007) used the name "Phobetina", but did not validate it under the International Commission on Zoological Nomenclature (1999). Specifically, Lacroix (2007) did not explicitly



FIGURES 35–37. *Phobetus comatus* LeConte, 1856 male. **35**, Dorsal habitus; **36**, oblique habitus; **37**, ventral habitus.

indicate "Phobetina" as intentionally new (Article 16.1) and the name is not accompanied by a description or definition or a bibliographic reference to such a published statement (Article 13.1). He listed *Phobetus* in the subtribe and included it in the tribe Tanyproctini (as Pachydemini). In their phylogenetic analysis of adult characters, Sanmartin & Martín-Piera (2003) cautiously considered *Phobetus* as a sister group to Palearctic Tanyproctini (as Pachydeminae), and noted differences in their larval morphology as well (see Sanmartin 2007). Eberle *et al*. (2019) noted that the taxon sampling of the previous study was limited and did not include *Phobetus* in their molecular phylogeny of Tanyproctini. We consider *Phobetus* not to be closely allied with any of the extralimital taxa currently included in Tanyproctini, as evidenced by the transverse procoxae, widely separated metatibial spurs, distinct abdominal sutures, and the relative lengths and membranous posterior margins of sternites that are not narrowed medially. Hardy (1978b) published the most recent identification key to *Phobetus*, but the genus is in need of revision.

Tribe Warwickiini Evans & Smith, new tribe

Figs. 38–40, 42, 45.
urn:lsid:zoobank.org:act:1C2D94C2-C79E-45E0-B7D8-5F18313E4B37

Type genus. *Warwickia* Smith & Evans, 2005.

Description. Melolonthinae. Antenna with 10 antennomeres, club with 6 lamellae. Labrum narrow and thin, free, located below clypeus, and extending beyond clypeal margin. Prothorax with membranous anterior pronotal margin. Abdomen with sutures distinct, sternites narrowed medially, 2–4 subequal in length, 5 somewhat longer, and posterior margins of 3–5 membranous; sternite and propygidium separated by suture; functional spiracles on segments 1–7, 1 in pleural membrane, and 2–7 in sternite. Legs with procoxae conical; protibia with apical spur, mesotibiae and metatibiae each with pair of apical spurs; metatibial spurs widely separated, located on each side of tarsal articulation; opposing tarsal claws similar and trifid.

Diagnosis. Warwickiini is distinguished from all other Nearctic melolonthine tribes by the following combination of characters: narrow, thin, free labrum located below clypeus, and extending beyond clypeal margin; abdominal sutures distinct with posterior margins, sternites narrowed medially with posterior margins of 3–5 membranous; conical procoxae, widely separated apical metatibial spurs, and trifid claws.

Composition. Warwickiini **new tribe** is comprised of the genus *Warwickia* Smith & Evans, 2005 (Figs. 38–40).

Habitat and distribution. The sole species in the tribe, *Warwickia pilosa* Sanderson, 1939, is known to occur in the Chihuahuan Desert of the Big Bend region in Texas and adjacent northern Chihuahua, Mexico.

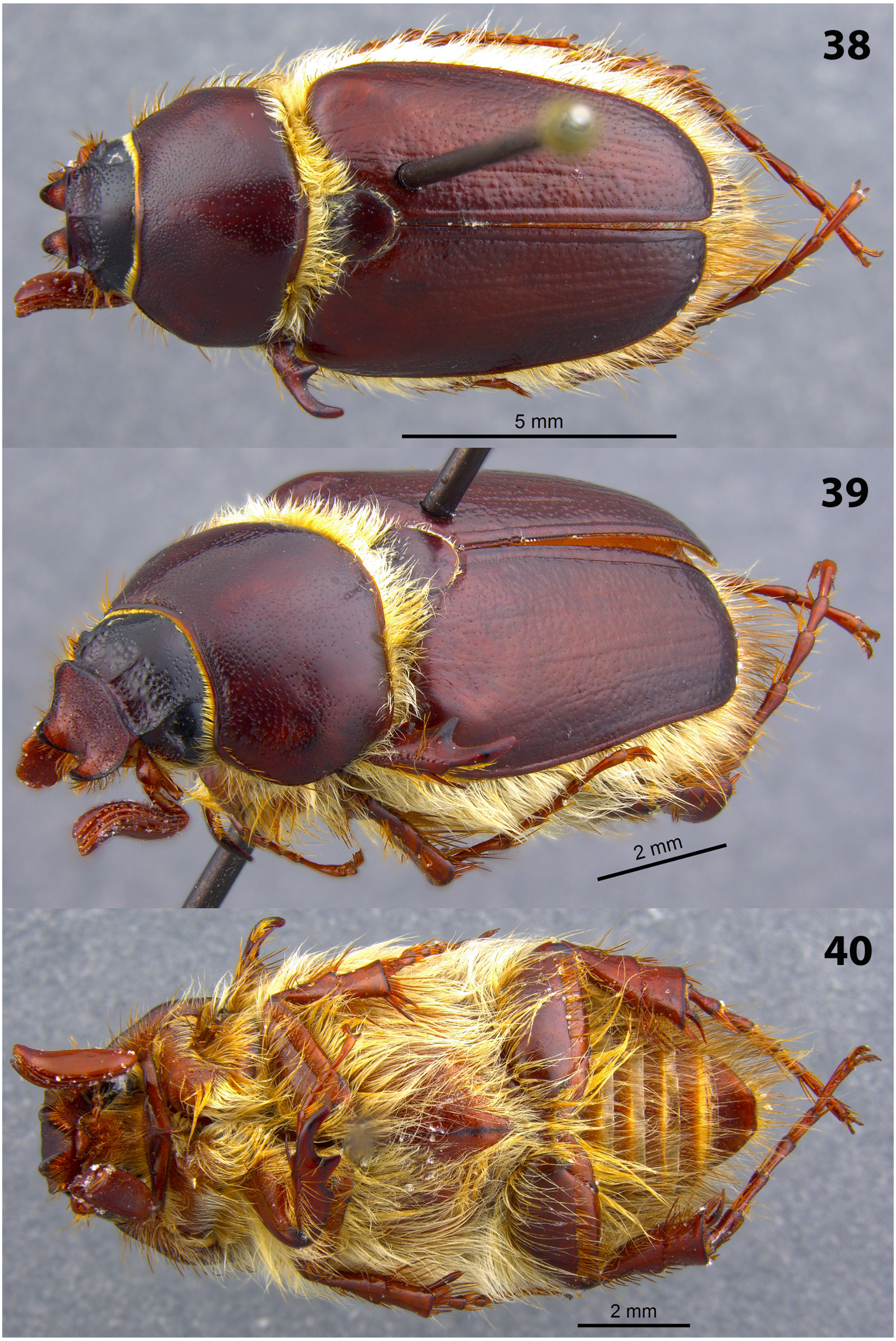
Habits. Males are attracted to lights in dry, sandy habitats dominated by mesquite during late spring and summer (Howden 1960; Evans, personal observation).

Remarks. Smith & Evans (2005) established *Warwickia* as a replacement name for *Benedictia* Sanderson, 1939, a junior homonym of *Benedictia* Dybowski, 1875 (Mollusca). Sanderson (1939) initially referred *Warwickia* (as *Benedictia*) to the Pleocominae, but Hardy (1978a) noted its superficial similarity to the South American tanyproctine *Acylochilus* (*Acylochilus*) and transferred it to the Tanyproctini (as Pachydemini), a tribe that does not occur in the Nearctic realm.

Revised status of Nearctic Melolonthini and Rhizotrogini

Since the catalogue of Dalla Torre (1913), the subtribes of Melolonthini (see Bouchard *et al*. 2011) have seldom been applied to the New World fauna. However, they have been used consistently in characterizing Old World melolonthines and were recently considered tribes in the latest catalogue for the Palaearctic Region (see Löbl & Löbl 2016).

In his review of the Melolonthini of North America, Howden (1968) noted the close relationship *Dinacoma* Casey, 1889*, Hypothyce* Howden, 1968*, Hypotrichia* LeConte, 1861*, Plectrodes* Horn, 1867*, Polyphylla* Harris, 1841*,* and *Thyce* LeConte, 1856 (including *Amblonoxia* Reitter, 1902) and, to a lesser degree, the indigenous *Phyllophaga* and adventive *Amphimallon* Latreille, 1825, and *Diplotaxis* (now in the Diplotaxini). His comments on the similarity between *Polyphylla pubescens* Cartwright, 1939 and some species of *Thyce* led Hardy (1974) to transfer that species into a new genus, *Polylamina* Hardy, 1974. A phylogenetic analysis (Coca-Abia 2000) of the

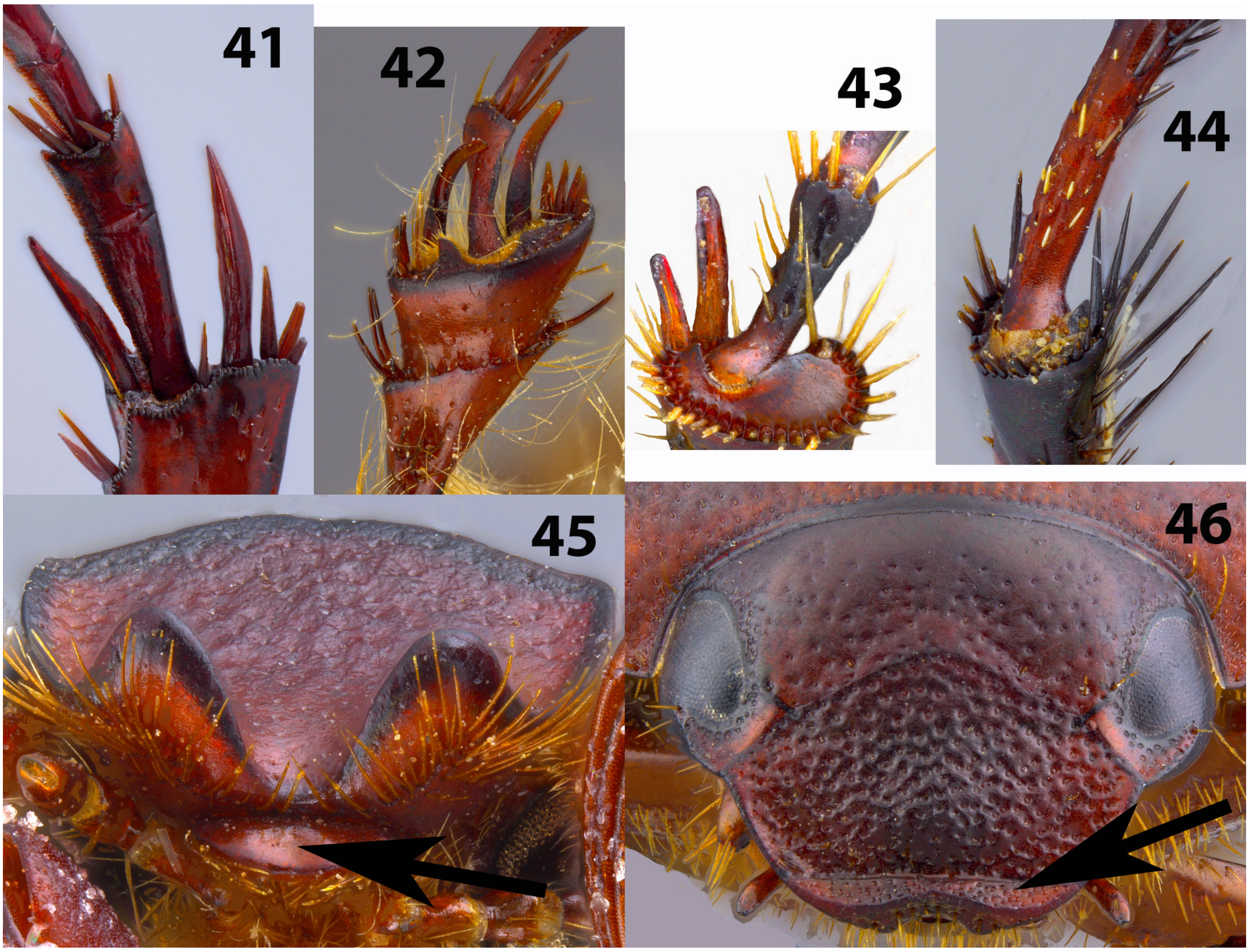


FIGURES 38–40. *Warwickia pilosa* (Sanderson, 1939) male. **38**, Dorsal habitus; **39**, oblique habitus; **40**, ventral habitus.

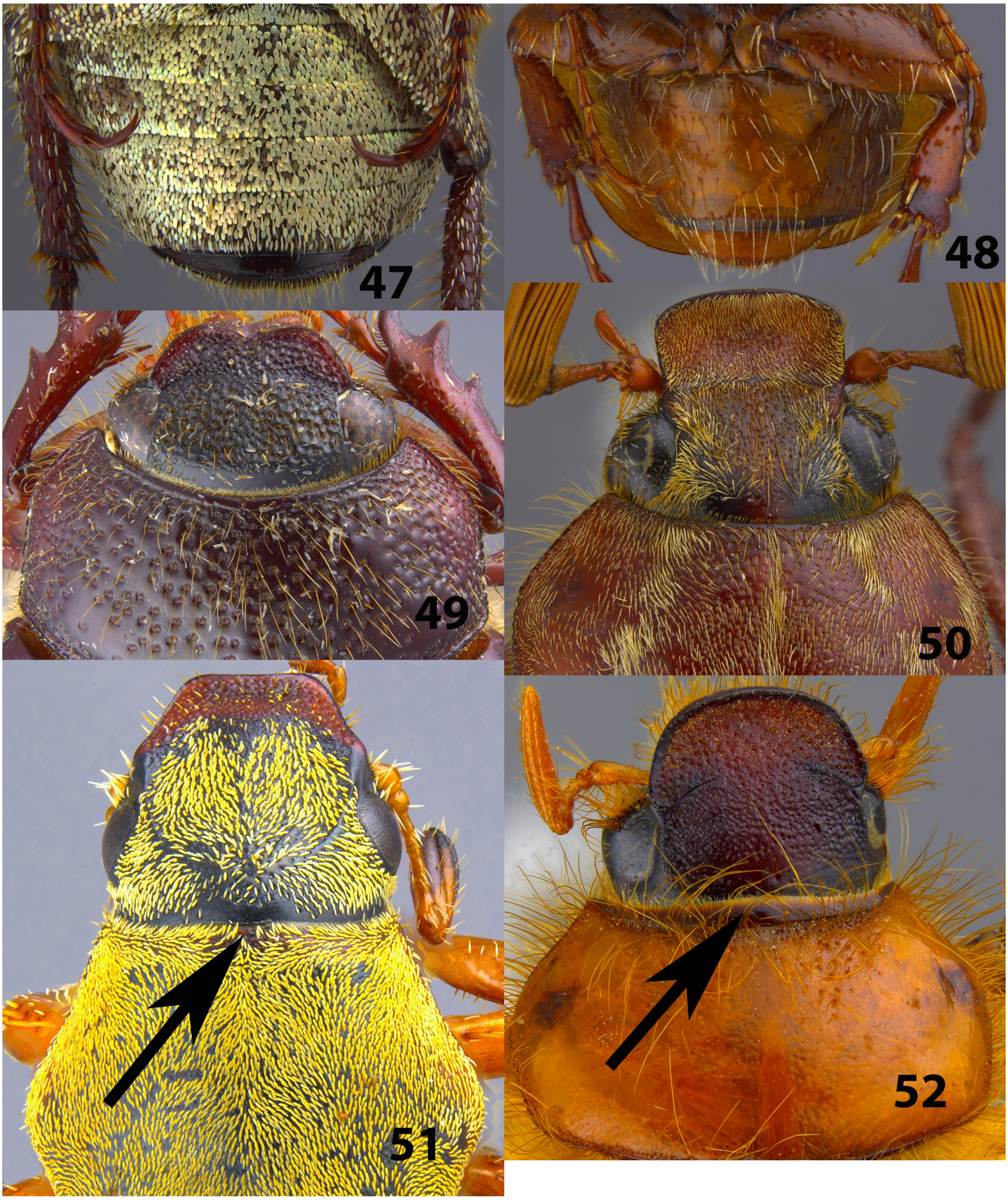
Nearctic melolonthines concluded that the monotypic *Polylamina* was a junior synyonym of *Polyphylla* and that it and *Amblonoxia* (as *Parathyce* Hardy, 1974), *Dinacoma*, *Hypothyce*, *Hypotrichia*, *Plectrodes*, and *Thyce* constituted a monophyletic clade (see also Coca-Abia 2007).

Coca-Abia (2007) also found moderate support for the tribe Rhizotrogini, but not for the monophyly of *Phyllophaga sensu lato* that includes the subgenera *Chirodines* Bates, 1888, *Chlaenobia* Blanchard, 1850, and *Listrochelus* Blanchard, 1850. Her analysis rejected the monophyly of the subgenera *Listrochelus* and *Phyllophaga*, suggested that *Trichesthes* Erichson, 1847 (as a genus) is paraphyletic, and noted that the relationships of the "phyllophagan" subgenera *Phytalus* Blanchard, 1851, *Eugastra* LeConte, 1856, and *Tostegoptera* Blanchard, 1851 are unresolved. However, the phylogenetic analyses of Rivera-Gasperín & Morón (2013, 2017a, 2017b) seem to support the elevation of three subgenera of *Phyllophaga* to full generic status, including *Chlaenobia*, *Triodonyx* Saylor, 1942, and *Listrochelus*. Concepts of the generic and subgeneric relationships within the New World Rhizotrogini will no doubt evolve with future studies on the group based on robust taxon sampling the includes Palaearctic rhizotrogine genera.

The results of our morphological examination of species in the Nearctic genera of Melolonthini (*sensu* Evans & Smith 2009) agrees with the analyses of Coca-Abia (2007). Thus, the tribe includes only the genera *Amblonoxia*, *Dinacoma*, *Hypothyce*, *Hypotrichia*, *Plectrodes*, *Polyphylla,* and *Thyce*, all of which are characterized by having a wide metepisternum (Fig. 54).



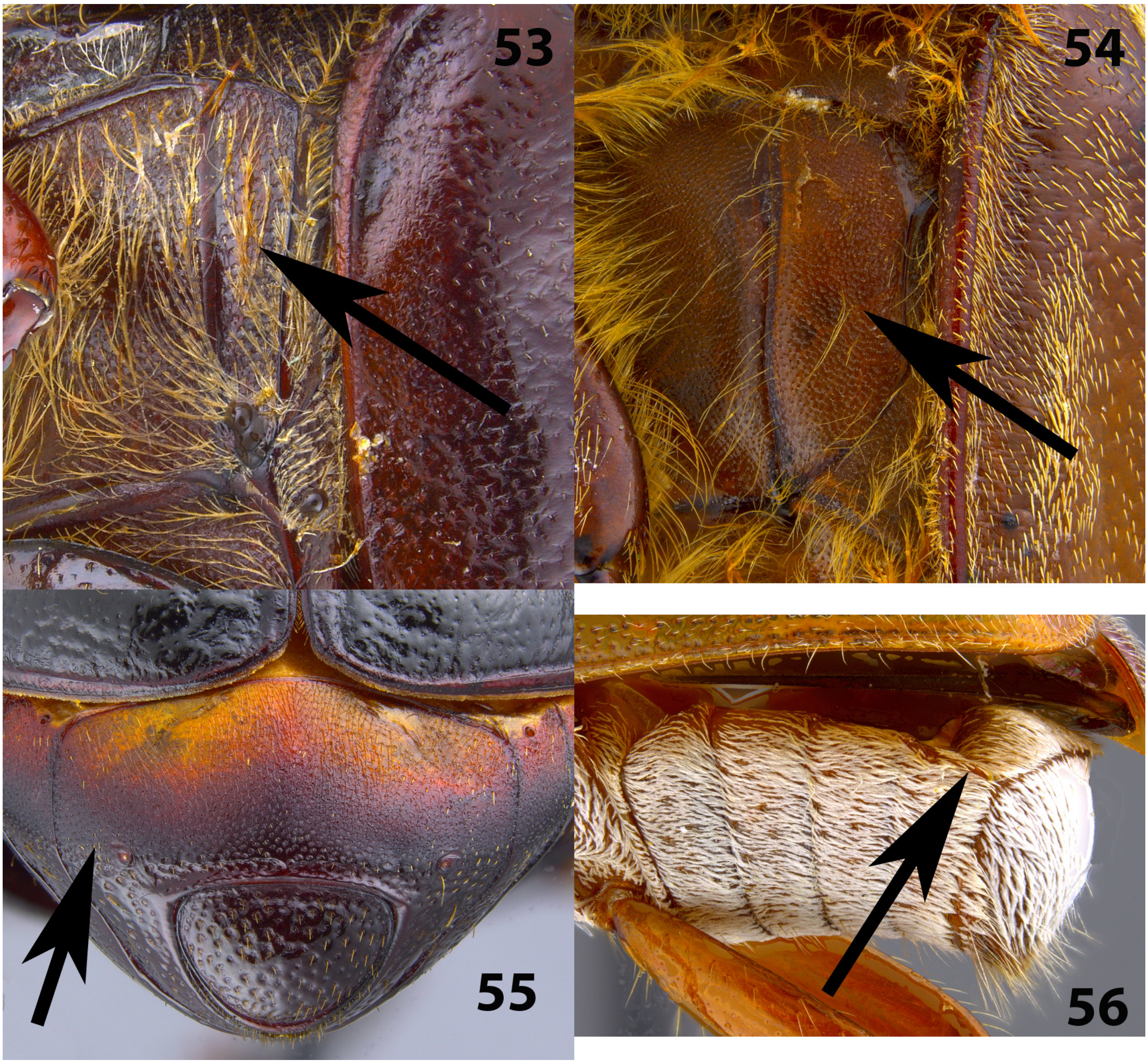
FIGURES 41–46. Characters of metatibia and clypeus. **41**, *Serica sericea* (Illiger, 1802) metatibial apex showing the spurs located above and below the tarsal articulation; **42**, *Warwickia pilosa* (Sanderson, 1939) metatibial apex showing the spurs located above and below the tarsal articulation; **43**, *Dichelonyx linearis* (Gyllenhal, 1817) metatibial apex showing the spurs both located below the tarsal articulation; **44**, *Macrodactylus subspinosus* (Fabricius, 1775) metatibial apex showing the absence of spurs in the males (a sexually dimorphic character); **45**, *Warwickia pilosa* showing the clypeus and labrum (arrow) as separate structures; **46**, *Serica sericea* clypeus showing the fused and coplanar labrum (arrow).



FIGURES 47–52. Characters of abdomen and pronotum. **47**, *Hoplia trifasciata* Say, 1825 ventral abdomen showing the distinct sutures; **48**, *Chnaunanthus flavipennis* (Horn, 1867) ventral abdomen showing the lack of visible sutures; **49**, *Phyllophaga hirticula* (Knoch, 1801) anterior pronotal margin without a translucent border; **50**, *Polyphylla variolosa* (Hentz, 1830) anterior pronotal margin without a translucent border; **51**, *Macrodactylus subspinosus* (Fabricius, 1775) anterior pronotal margin with a translucent border somewhat obscured by scales; **52**, *Phobetus comatus* LeConte, 1856 anterior pronotal margin with a clearly-defined translucent border.

Further, we recognize the Nearctic Rhizotrogini to include the indigenous "phyllophagan" genera *Chlaenobia*, *Listrochelus*, *Phyllophaga* (including subgenera *Cnemarachis* Saylor, 1942, *Eugastra*, *Phyllophaga*, *Phytalus*, *Tostegoptera*, *Trichesthes*) and *Triodonyx*, as well as *Fossocarus*, *Gronocarus*, and the adventive *Amphimallon*. *Madiniella*, a Neotropical genus endemic to Martinique and formerly placed in Tanyproctini, should also be classified in the tribe Rhizotrogini. Genera in the Rhizotrogini are distinguished from those in the Melolonthini by having a narrow metepisternum (Fig. 53).

Rivera-Gasperín & Morón (2013) erected the subtribe Triodonina (of the tribe Melolonthini; containing only the genus *Triodonyx*) based on their phylogenetic analysis. As a result of our classification changes, we are placing Triodonina in synonymy with Rhizotrogini pending a thorough phylogenetic analysis of the worldwide genera in this tribe.



FIGURES 53–56. Characters of thorax and abdomen. **53**, *Phyllophaga hirticula* (Knoch, 1801) narrow metepisternum (arrow); **54**, *Polyphylla variolosa* (Hentz, 1830) wide metepisternum (arrow) (with setae removed to view structure); **55**, *Diplotaxis tristis* Kirby, 1837 apical view with propygidium fused to sternite (arrow); **56**, *Dichelonyx linearis* (Gyllenhal, 1817) lateral abdomen with suture (arrow) between propygidium and sternite.

Identification key to the tribes of the Nearctic Melolonthinae

See Table 2 for a list of the Nearctic tribes and genera. This key will also work for all Melolonthinae occurring in Central America and the West Indies.

1 Metatibial spurs located above and below the tarsal articulation so that the first metatarsomere can pass between them (Fig. 41–42) (Sericini, Warwickiini) 2

-. Metatibial spurs both located either below the tarsal articulation so that the metatarsomere passes over them (Figs. 43), with the upper spur located adjacent to the tarsal articulation (Fig. 57), or completely absent (males of several genera of Macrodactylini; Fig. 44) (Acomini, Chnaunanthini, Dichelonychini, Diplotaxini, Hopliini, Macrodactylini, Melolonthini, Phobetusini, Rhizotrogini) 3

2 Labrum located below the clypeus (Fig. 45), visible beyond the clypeal margin . . . . Warwickiini **new tribe**

- Labrum coplanar and fused to the anterior margin of the clypeus to form a clypeolabral margin (Fig. 46); clypeolabral suture evident, or indicated laterally as a notch on the margin . . . . Sericini

3 Abdominal sutures distinct or effaced only at middle (Fig. 47) (Acomini, Dichelonychini, Diplotaxini, Hopliini, Macrodactylini, Melolonthini, Phobetusini, Rhizotrogini) 4

- Abdominal sutures entirely effaced ventrally, traces sometimes visible at sides (Fig. 48) . . . . Chnaunanthini **new tribe**

4 Metatarsus with a single, well-developed claw . . . . Hopliini

- Metatarsus with a pair of claws (*Acoma* females may have a single, undeveloped claw) (Acomini, Dichelonychini, Diplotaxini, Macrodactylini, Melolonthini, Phobetusini, Rhizotrogini) 5

5 Anterior pronotal margin without translucent border at middle (Figs. 49–50); abdominal sutures effaced medially (males of *Plectrodes* Horn, 1867 distinct and imbricate) (Melolonthini, Rhizotrogini) 6

- Anterior pronotal margin with translucent border at middle (Figs. 51–52); abdominal sutures distinct medially (Acomini, Dichelonychini, Diplotaxini, Macrodactylini, Phobetusini) 7

6 Metepisternum narrow (Fig. 53) . . . . Rhizotrogini

- Metepisterum wide (Fig. 54) . . . . Melolonthini

7 Propygidium and fifth tergite forming a sclerotized ring, without any trace of a suture (Fig. 55); pygidium small, round, not partially covered by elytra . . . . Diplotaxini

- Propygidium and fifth tergite joined with at least a trace of a suture (Fig. 56); pygidium large, triangular, often partially covered by elytra (Acomini, Dichelonychini, Macrodactylini, Phobetusini) 8

8 Metatibial spurs set with one below and one next to tarsal articulation (Fig. 57) (Acomini, Phobetusini) 9

- Metatibial spurs set below tarsal articulation (Fig. 58) or absent (Fig. 44) (Dichelonychini, Macrodactylini) 10

9 Claws simple . . . . Acomini **new tribe**

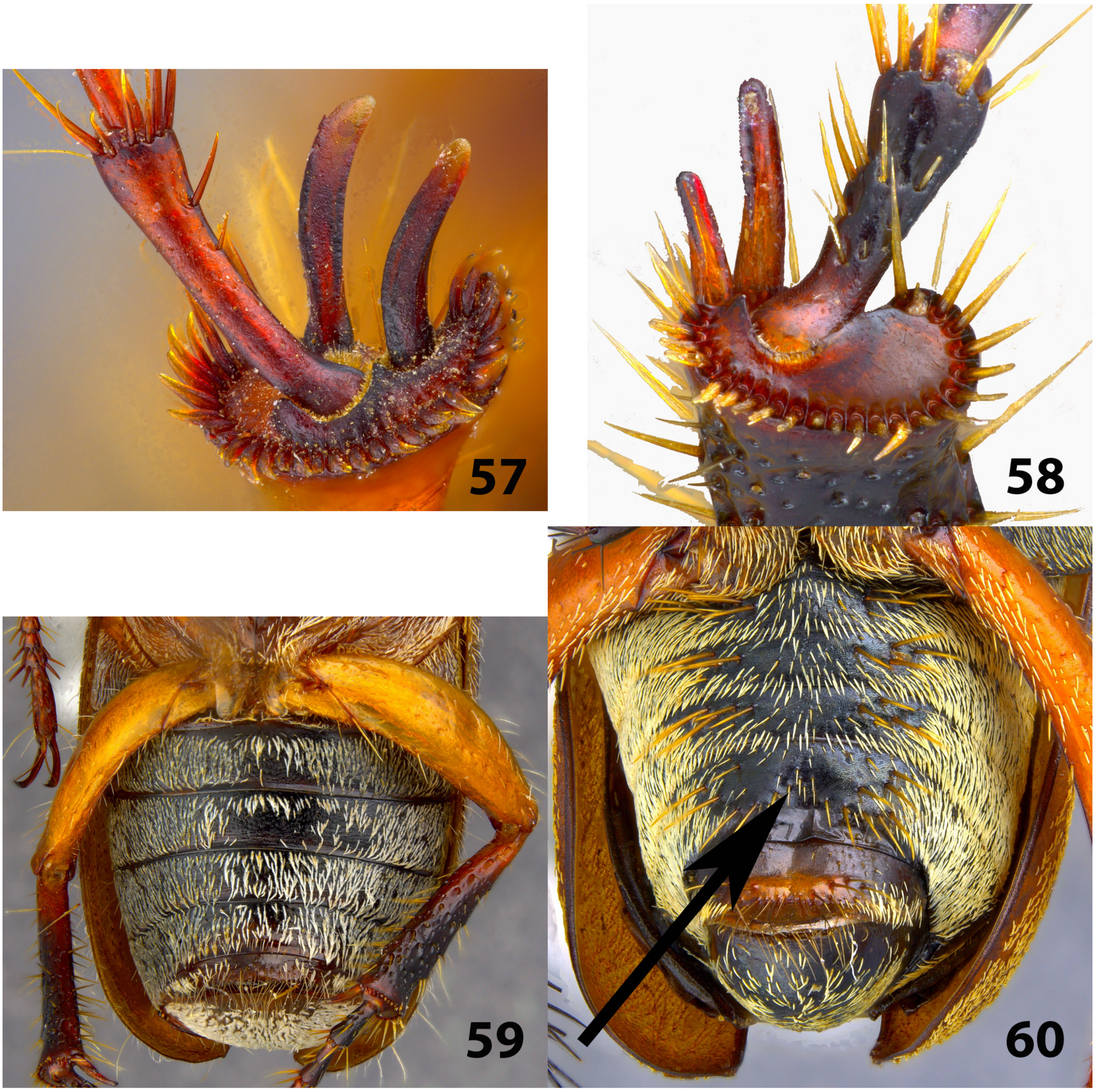
- Claws cleft . . . . Phobetusini **new tribe**

10 Abdominal sternites subequal in length (Fig. 59) . . . . Dichelonychini

- Abdominal sternite 5 longer than each of the preceding sternites (Fig. 60) . . . . Macrodactylini

TABLE 2. The tribes and genera of Nearctic Melolonthinae.

Tribe	Genera
Acomini	*Acoma* Casey, 1889
Chnaunanthini	*Chaunocolus* Saylor, 1937, *Chnaunanthus* Burmeister, 1844
Dichelonychini	*Coenonycha* Horn, 1876, *Dichelonyx* Harris, 1827, *Gymnopyge* Linell, 1896
Diplotaxini	*Diplotaxis* Kirby, 1837
Hopliini	*Hoplia* Illiger, 1803
Macrodactylini	*Isonychus* Mannerheim, 1829, *Macrodactylus* Dejean, 1821, *Plectris* LePeletier & Serville, 1828
Melolonthini	*Amblonoxia* Reitter, 1902, *Dinacoma* Casey, 1889, *Hypothyce* Howden, 1968, *Hypotrichia* LeConte, 1861, *Plectrodes* Horn, 1867, *Polyphylla* Harris, 1841, *Thyce* LeConte, 1856
Phobetusini	*Phobetus* LeConte, 1856
Rhizotrogini	*Amphimallon* Latreille, 1825, *Fossocarus* Howden, 1961, *Gronocarus* Schaeffer, 1927, *Listrochelus* Blanchard, 1851, *Phyllophaga* Harris, 1827 (including subgenera *Chlaenobia* Blanchard, 1850, *Cnemarachis* Saylor, 1942, *Eugastra* LeConte, 1956, *Phyllophaga*, *Phytalus* Blanchard, 1851, *Tostegoptera* Blanchard, 1851, *Trichesthes* Erichson, 1847), and *Triodonyx* Saylor, 1942
Sericini	*Maladera* Mulsant & Rey, 1871, *Nipponoserica* Nomura, 1973, *Serica* MacLeay, 1819
Warwickiini	*Warwickia* Smith & Evans, 2005



FIGURES 57–60. Characters of metatibia and abdomen. **57**, *Phobetus comatus* LeConte, 1856 metatibial apex showing one spur below and one spur next to tarsal articulation; **58**, *Dichelonyx linearis* (Gyllenhal, 1817) metatibial apex showing both spurs below tarsal articulation; **59**, *Dichelonyx linearis* ventral abdomen showing the subequal sternites; **60**, *Macrodactylus subspinosus* (Fabricius, 1775) ventral abdomen showing the elongate sternite 5 (arrow).

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